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Chimpanzees (*Pan troglodytes*) in savanna landscapes

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[Correction added on October 15, 2021 after first online publication: figure caption added for the image in box 2]

Abstract

Chimpanzees (*Pan troglodytes*) are the only great apes that inhabit hot, dry, and open savannas. We review the environmental pressures of savannas on chimpanzees, such as food and water scarcity, and the evidence for chimpanzees' behavioral responses to these landscapes. In our analysis, savannas were generally associated with low chimpanzee population densities and large home ranges. In addition, thermoregulatory behaviors that likely reduce hyperthermia risk, such as cave use, were frequently observed in the hottest and driest savanna landscapes. We hypothesize that such responses are evidence of a "savanna landscape effect" in chimpanzees and offer pathways for future research to understand its evolutionary processes and mechanisms. We conclude by discussing the significance of research on savanna chimpanzees to modeling the evolution of early hominin traits and informing conservation programs for these endangered apes.

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KEYWORDS
behavioral flexibility, dry environments, mosaic vegetation, *Pan troglodytes*, primates, seasonality

1 | INTRODUCTION

Paleoecological reconstructions show that some early hominins occupied mosaic savanna landscapes (reviewed in Domínguez-Rodrigo[1]). The effects of such open and dry landscapes and the environmental pressures associated with them may have contributed to the evolutionary split of the *Homo* and *Pan* lineages.[1–5] This early version of the "savanna hypothesis"[1] was combined with a referential modeling approach to help reconstruct the behavior of extinct hominins with a particular focus on the last common ancestor (LCA).[6–8] Embracing that perspective, primatologists since the 1960s have studied chimpanzees (*P. troglodytes*) in open and dry environments (Box 1) and have often referred to them as "savanna chimpanzees."[4]

The landscape approach (e.g., Turner[9]) is useful for comparing and contrasting chimpanzees in savanna and forest environments. Landscapes encompass a variety of vegetation types, watersheds, topographies, and human land uses that affect individuals over the life course and populations across generations. Landscapes for chimpanzees are defined at spatial scales that are, at a minimum, as large as a unit-group's or community's home range (Table S1) and may include areas up to thousands of square kilometers (hereafter, we use unit-group and community interchangeably). Savanna chimpanzee home ranges approach or exceed 100 km^2 whereas chimpanzees in more forested landscapes have home ranges of about 3–30 km^2 (see Table S1).[10]

Savanna chimpanzees are taxonomically indistinguishable from other conspecifics (Supporting Information) but they live in climates characterized by low annual rainfall, high rainfall seasonality, and high temperatures. For heuristic purposes, we use the term forest chimpanzees to refer to conspecifics in environments with higher forest cover and higher annual rainfall (forest mosaics and dense forests: sensu van Leeuwen et al.[11]), and we recognize that the range of landscapes for chimpanzees is more than binary (see Savanna Chimpanzees section).

This review synthesizes research on chimpanzees in savanna landscapes to examine the state of the field and motivate new research trajectories. The larger body of work on wild chimpanzees is forest biased (Table S2), as primatologists have historically focused on observational data from habituated study subjects[12] and there have been fewer efforts to habituate savanna chimpanzee communities. In this paper, we will (1) describe characteristics of savanna landscapes and savanna chimpanzees, (2) review environmental conditions that have the potential to create challenges for chimpanzees in savannas concerning the availability of nesting materials, food, water, and refuges from hot temperatures and potential predators, (3) discuss the implications of this evidence for referential and conceptual modeling in paleoanthropology,[4,8] as well as savanna chimpanzee conservation (Box 2), and (4) recommend directions for future research.

2 | SAVANNAS

A comprehensive recognition of the abiotic and biotic components of savannas is needed to fully understand the behavior and ecology of chimpanzees living in these environments, and the utility of savanna chimpanzees to modeling hominin evolution. Notably, each ecological process (e.g., herbivory; Supporting Information) that we describe does not exclusively occur in savanna landscapes but interactions among such processes in these landscapes are in many ways biologically distinct from those of more forested areas. While terminology inconsistencies have been a source of confusion in scientific studies,[1,11,13,14] we consider savanna landscapes to be those primarily consisting of fire-adapted trees, shrubs, and C_4 grasses, with a mostly open tree canopy and an understory of nearly continuous cover of grasses and sedges.[1,4,13,15–18] Woody vegetation (trees, shrubs and lianas) provides chimpanzees with food, refuge, and materials for nest construction and tool manufacture but woody biomass is less abundant in savannas than in more forested landscapes.[18–20] Savanna landscapes occupied by chimpanzees are a mosaic of different vegetation types that can be divided into three major categories: (1) open and deciduous (e.g., woodland, wooded grassland, and grassland; hereafter "open vegetation"), (2) closed and evergreen (e.g., gallery/riparian or thicket forest; hereafter "closed vegetation"), and (3) a transitional "ecotone" category for vegetation that is neither mostly open nor mostly closed. Closed vegetation types lack the continuous C_4 grass understory and cover a small proportion of the landscape.[18–20] Due to inconsistencies in how savannas are defined, chimpanzee researchers have used the term savanna to describe dry tropical landscapes with a wide range of forest covers but most often for areas at the low end of the spectrum (e.g., <12.5% closed vegetation cover).[11]

2.1 | Hydrologic cycle

The hydrologic cycle is a major determinant of savanna landscapes.[18,19] Overall, savanna climates are characterized by low mean annual rainfall (range: 100–1550 mm) and high rainfall seasonality.[19,21] The seasonal rains are often concentrated in one long rainy season, but two short rainy seasons characterize some savanna environments.[18,19] Savanna chimpanzees have not been observed to inhabit areas with less than 750 mm of average annual rainfall, and most populations live in climates with one rainy season, with the known exceptions of Ishasha in Democratic Republic of Congo and Semliki in Uganda.[11] Water is oftentimes in limited supply in savannas, particularly in climates with one dry season or in watersheds with low water tables and little runoff.[21] During dry months, surface water evaporates and is eventually only accessible at permanent sources, such as ground-fed springs and seeps or larger rivers and streams with inflow from regional watersheds. During

BOX 1 Origins of savanna landscape chimpanzee research (1961–1979)

Research on savanna chimpanzees traces back to Japanese primatologists Kinji Imanishi and Junichiro Itani. Here, we take a closer look at this earliest work and briefly describe the savanna chimpanzee projects that were first established in East and West Africa. In 1958, Imanishi and Itani went to Africa to study our closest relatives, gorillas, and chimpanzees, with the intent to use long-term observations on individual animals (this was a unique method in the 1950s developed by Japanese primatologists during their studies of wild Japanese macaques [*Macaca fuscata*]). The main aims of their study were to describe nonhuman primate behavior and ecology, and apply these observations to reconstructions of early hominin societies and ecologies.[235] In 1961, Japanese primatologists pioneered savanna chimpanzee research in the miombo woodlands of the northern part of the Greater Mahale Ecosystem. They conducted research at Kabogo Point on the lakeshore,[236] Kasakati,[237] and Filabanga,[89] and were interested in these savanna environments for their hypothesized similarities to the environments occupied by *Australopithecus* spp.[235]

In the early 1960s, Kano tried to habituate savanna chimpanzees at Filabanga[89] but did not succeed. Moreover, he discovered evidence for seasonal shifts in ranging behavior at Filabanga,[89] which may have further hindered habituation. In 1965, Itani and Suzuki anecdotally observed a large and relatively stable group of chimpanzees at Filabanga.[161] Although the composition and arrangement of this group indicated that chimpanzees had a complex social structure, primatologists had disagreed on the exact nature of this social system.[161] These observations contributed to the landmark discovery that chimpanzees form a stable unit-group (community), which splits into temporal unit-subgroups (parties).[159] These early researchers showed that savanna chimpanzees, like their forest counterparts, hunt and eat mammals, and use tools to capture ants and termites.[59,237–240] Additionally, low population densities and large home ranges were reported by early savanna chimpanzee researchers.[5,57,89,241] Kano made the first extensive survey from 1965 to 1967 to estimate savanna population sizes in Tanzania.[52,57] In West Africa, de Bournonville[242] conducted a regional survey in the savannas of Senegal and Brewer established a reintroduction project for rescued chimpanzees at Assirik in Niokolo Koba National Park,[243] also in Senegal. The first long-term research project on savanna chimpanzees in West Africa was established at Assirik by McGrew, Tutin, and Baldwin, and was active from 1976 to 1979.[29,45,160] The low population densities led to very low encounter rates and made habituation of savanna chimpanzees exceedingly challenging for these pioneer research projects in Tanzania and Senegal.[160,244] The resulting slow pace of progress at these sites and the consequent difficulty of achieving break-through discoveries made it hard to obtain funding to continue research[244] (W. C. McGrew personal communication). The successful habituation of higher-density chimpanzees in more forested landscapes at Gombe,[59] Mahale,[91] and Bossou[245] enabled detailed behavioral observations that led chimpanzee researchers to shift their attention from savannas to more forested sites (see Research Bias in the Supporting Information).

In the 1980s, other researchers studied savanna chimpanzees in previously neglected areas, such as Moore at Bafing in Mali,[246,247] Sept at Ishasha in Democratic Republic of Congo,[81] and Hunt at Semliki in Uganda.[46] While six decades have passed since the first projects launched, habituated savanna chimpanzees have been accessible only since 2005 when adult males at Fongoli could be reliably sampled for a full day, from sunrise to sunset.[248] In 2018, Issa joined Fongoli as the second long-term study site with habituated chimpanzees.[249] The habituation process continues to advance at Semliki; most unit-group members are semi-habituated to researchers and a small set of individuals can be systematically observed throughout an entire day[132] (K.D. Hunt, personal communication). Now, it is possible to evaluate inter-group behavioral variation for habituated savanna chimpanzees.

the dry season, preformed water is more difficult for savanna chimpanzees to access in deciduous plants.[18,22] Leafy sources of protein are also affected by rainfall,[23] and expected to be less abundant during the dry season. While rainfall is likely the most important climate determinant of savanna landscapes,[20] it can work synergistically with temperature and evapotranspiration to shape the abundance and distribution of grasses and trees.[24]

2.2 | Edaphic factors

Edaphic factors such as soil particle type (e.g., silty, sandy), soil fertility, and landscape topography additionally affect water flow, soil water availability, and vegetation cover in savannas.[15,17–19] In addition, surface bedrock or hardpan can increase rocky area cover, decrease soil depth, and lower soil fertility in ways that limit tree growth.[18,25] Several West African chimpanzee study sites are especially dry and open due to lateritic pans (Figure 1).

2.3 | Open vegetation

The open vegetation that dominates savanna landscapes (reviewed in van Leeuwen et al.[11]) is characterized by low tree density, low leaf area, high understory light, C_4 grasses, and short trees (range: 2–6 m), but see miombo woodlands for an exception to tree height.[16,18,26,27] It is challenging to classify mixed savanna-forest or ecotone landscapes when open- and closed-vegetation are proportionally similar.[15]

BOX 2 Savanna chimpanzee conservation

The chimpanzee is an endangered species with populations in decline across Africa.[10] Savanna populations enrich our understanding of chimpanzee ecology, behavioral flexibility, and human evolution (this review). They are often embedded in cultural traditions (e.g., hunting taboos),[56,146] provide an ecosystem service with seed dispersal,[47,90,92] and are potential reservoirs for cultural diversity.[140] Thus, research and management practices aiming to preserve savanna chimpanzees are worthy of support.

Similar to the bias in behavioral research towards more forested landscapes, survey and conservation efforts have disproportionately neglected savanna landscapes (e.g., Ivory Coast,[250] Liberia,[251] Sierra Leone[252]). More recently, studies in Guinea's Fouta Djallon,[204] and the Kedougou region of Senegal,[146] have identified larger savanna populations than previously estimated. Similar to West Africa, little surveying has been conducted in the savanna landscapes of the eastern chimpanzee range.[52,57,253–255] This dearth of information significantly affects statistical models of chimpanzee population size and habitat suitability that are routinely used in conservation planning,[145] as smaller sample sizes lower predictive power. Furthermore, modeling habitat suitability for savanna chimpanzees poses special challenges, as not all determinants of chimpanzee occupation are easily extracted from remotely sensed data in savanna landscapes (e.g., proximity to or permanence of water sources). For these reasons, more granular and landscape-level models of chimpanzee ecology may be key tools for identifying and protecting biological corridors between protected and unprotected areas, or other forms of species conservation planning.

Most savanna chimpanzees reside in lands outside of national parks,[146,256] where they share spaces with people. Conflicts between humans and chimpanzees (e.g., competition over natural resources, chimpanzee killings or displacements) are especially pronounced in unprotected areas.[257,258] Like chimpanzees elsewhere, savanna populations experience habitat loss and degradation from activities such as timber and mineral extraction (Figure Box 2), charcoal production, agriculture (crops and livestock), infrastructure development, and settlement expansions or relocations.[146,258–260] Little is known about crop-feeding in savanna chimpanzees. It rarely occurs in Senegal (Fongoli,[27] Heremakhono[98]) and there are no reports of crop-feeding in Tanzania; nonetheless, it is a potential source of conflict with the people who live alongside them. In addition, savanna chimpanzees in the hottest and driest places experience competition with people and their livestock over drinking water (Dindefelo).[260]

Figure Box 2 Chimpanzees at Fongoli in Senegal drink polluted water in mining pits. Photo credit: J. Pruetz.

Addressing these conservation and sustainability issues requires the full inclusion of local people, including but not limited to host country scholars, students, and managers of unprotected and protected areas, into applied research and conservation practice.[227,228] Because local expertise is essential to building regional and national chimpanzee conservation action plans, a key conservation outcome could be the establishment of local primatology training programs involving global and fully engaged partnerships. Moreover, the recent creation of the African Society of Primatology is a major achievement, as this professional society fosters the exchange of conservation research, provides networking opportunities for African primatologists, and supports the implementation of primatology curricula in African universities.

Climate change will likely impact savanna chimpanzees, as climate models predict that rainfall will become more seasonal, temperatures will be hotter, and surface water availability will decrease for parts of the species' range.[261–263] Understanding adjustments specific to savanna chimpanzees may become more relevant as forest landscapes become drier and more seasonal. In the future, savanna chimpanzees will likely endure more extreme conditions, providing insights into the limits of their climate tolerance. In this sense, they are positioned at the frontier of climate change scenarios and may act as sentinels for the species.

FIGURE 1 Chimpanzees at Fongoli walking on the laterite pan that limits tree growth. Seasonal bush fires sweep through these grasslands each year and incinerate most senesced vegetation. These areas remain open until the rains return and catalyze plant growth. Photo credit: U. Villalobos-Flores

In these cases, site descriptions that specify vegetation types and their relative land covers provide context for their characterization.[11,25,28–30]

2.4 | Fire

Natural or anthropogenic bush fires, or both, maintain many mixed tree-grass systems, including those important to savanna chimpanzees,[22,31] and presumably to early hominins.[32] These fires produce variable burn footprints and intensities, and occur at regular intervals of ~1–7 years.[20,33–35] Burning processes sometimes reduce tree cover (e.g., through sapling die-off) and affect the functional traits of plants (e.g., corky bark, apical bud sheaths, post-fire re-sprouting, and seed germination).[18,32,34,36]

3 | SAVANNA CHIMPANZEES

Several nonhuman primates flexibly respond or are adapted to the environmental conditions of savanna landscapes.[37–40] The biographical ranges of nearly all primate species (99%) include forest landscapes (Table S3). Savanna, grassland, and shrubland landscapes occur within the range of 57% of primate species (Figure 2; Table S3), but they are the dominant landscapes for only 20% of species,[43] and use of open vegetation types has been reported for 17% of species.[44] African great apes use open vegetation types, but chimpanzees are more ecologically flexible in that they also inhabit landscapes that can be hotter, drier, and more open than those of bonobos or gorillas. Many of these savanna chimpanzees extensively use open vegetation types for feeding, traveling, resting, sleeping, and socializing on a daily or near daily basis.[28,30,45–47] Bonobos (*P. paniscus*) mainly live in densely forested landscapes (Table S3), but they also occur in forest-savanna mosaics, where they occasionally forage within grassland vegetation and tree-grass ecotone.[48,49]At the Manzano study site in the Democratic Republic of Congo, about 42% of the landscape is open vegetation but the bonobos allocate about 97% of their time in forest areas.[50] Gorillas (*Gorilla* sp.) in forest-savanna landscapes sporadically forage and rest in dry grassland vegetation,[51] and eastern gorillas (*G. beringei*) use montane open landscapes (Table S3) that are climatically different from the edaphic savannas occupied by chimpanzees.

Chimpanzees are distributed along a land cover continuum from savanna to forest.[1,11,52] Moreover, these landscapes exhibit vegetation physiognomies ranging from high homogeneity to high heterogeneity. We are unable to make granular comparisons of relative vegetation cover across chimpanzee study sites due to definition inconsistencies and the tendency for remote-sensing data sets (e.g., Hansen's tree cover) to flatten variation within and among vegetation types into a single value (e.g., % tree cover).[11,53] These issues were recently explored in a post hoc analysis of vegetation classification,[11] where the authors found that chimpanzee researchers have tended to use the term "savanna" for sites with very low forest cover (<12.5%) and the lowest averages for annual rainfall (<1360 mm) (Figure 3).[11] However, minimum and maximum tree-cover thresholds of 10%–60% (evergreen and deciduous tree cover, tree height > 2 m,[55] cf. forest cover) have also been used to classify landscapes inhabited by chimpanzees as savannas.[56] The first and more pervasive usage is effective for identifying environmental pressures associated with the most open, dry, and hot environments for chimpanzees, while the second interpretation accommodates a wider variety of open landscapes. We use the first interpretation hereafter to review environmental conditions in the hottest, driest, and most open landscapes, and acknowledge that there are limitations to applying dichotomous labels (e.g., either savanna or forest) to highly complex landscapes that fall along a continuum of land-cover types.[21,35,57]

4 | LANDSCAPE CONDITIONS AND POTENTIAL CHALLENGES

Savanna chimpanzees are ideal subjects for studying physical and behavioral adjustments or adaptations to hot, dry, and open environments, as several resources are expected to occur at relatively low

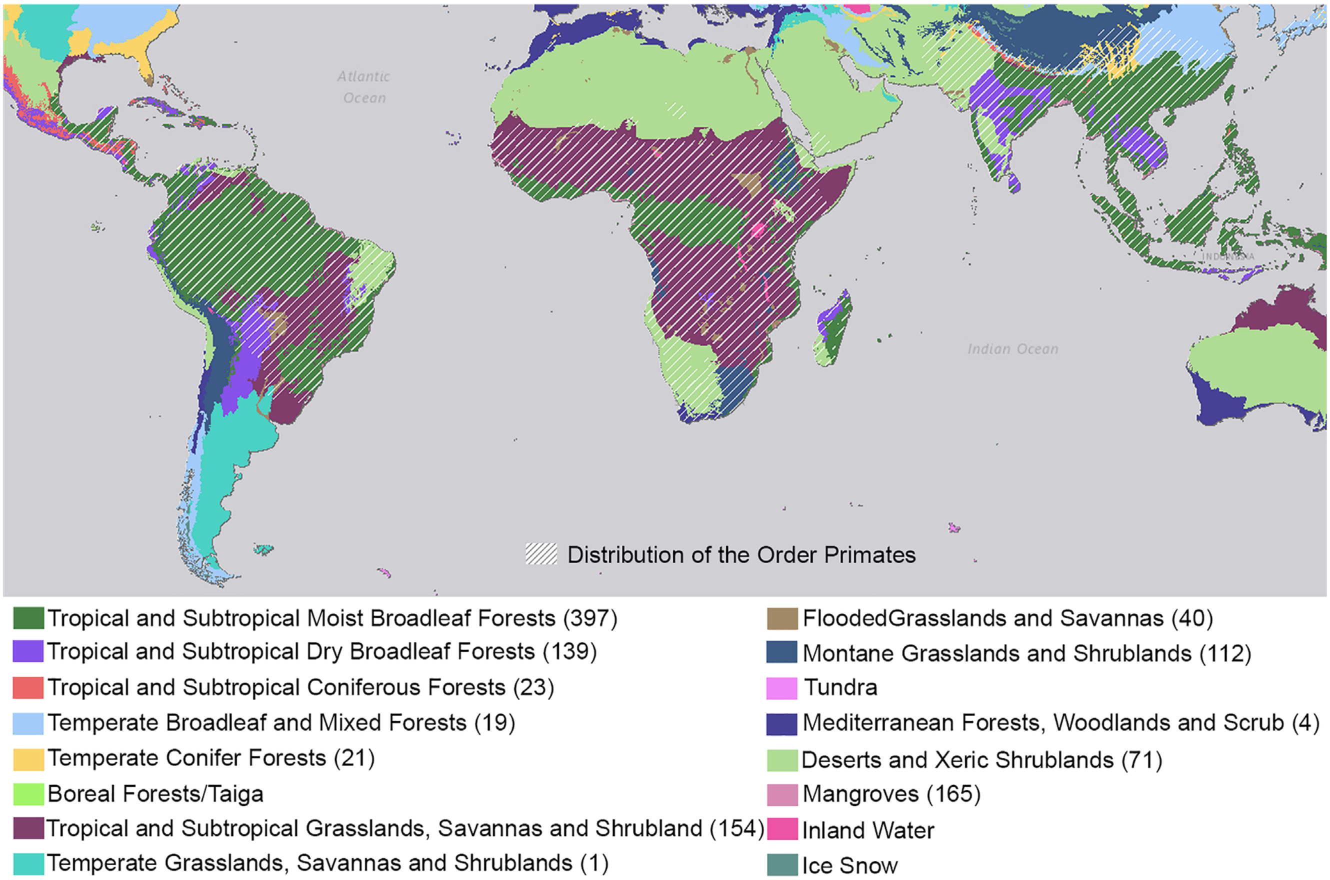

FIGURE 2 Primates' geographical distribution and ecoregions.[41,42] Each number in the legend indicates the number of primate species found in a particular terrestrial ecoregion (Table S3). Primates are found in a wide variety of biomes, as 12 ecoregions occur within the primate range. Although the ranges of around 57% of species overlap with savannas or other dry-open ecoregions, only ∼17% are recorded using such areas (Supporting Information)

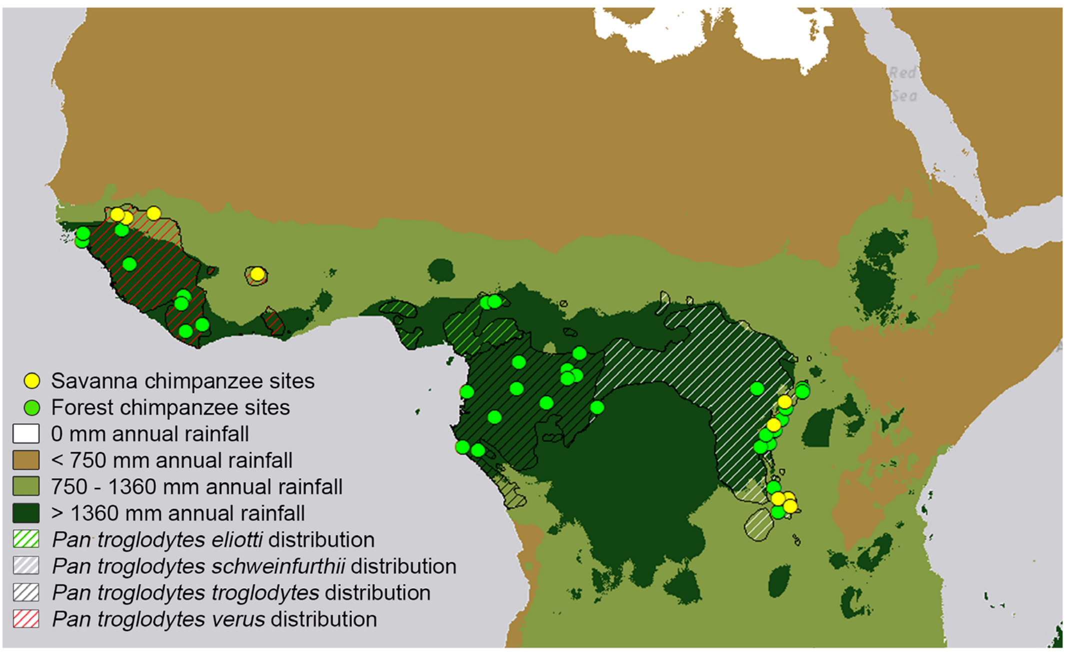

FIGURE 3 Geographic distribution of chimpanzees (*Pan troglodytes*)[54] in savanna and forest landscapes across Africa relative to the minimum threshold of annual rainfall (Worldclim),[11,54,264] and indicating potential new sites for future research on savanna chimpanzees. This figure is modified from Reference 11 under a Creative Commons Attribution 4.0 International License

densities for them. For example, while strong seasonality is challenging for primates in general,[58] it could be especially pronounced in savanna landscapes where water as well as leafy and woody vegetation are relatively scarce for several months of the year. In this section, we review the evidence for overall or seasonal scarcity of nesting resources, food, water, and refuges from hot temperatures and potential predators, and the effects that such resource scarcity may have on behavior. Furthermore, we describe findings that contradict some reductionist views about resource scarcity in savanna landscapes.

4.1 | Nesting resources

Weaned chimpanzees build nests to sleep at night and to rest during the day.[59] Nests also function to aid in thermoregulation, improve comfort during sleep, and minimize predation risk (see Supporting Information for predation risk in savanna landscapes) or pathogen and pest exposure, all of which may increase sleep quality.[60–66] Chimpanzees show complex capacities for manipulating and selecting nest materials,[60,61,64,66,67] can vary their nest shape and architecture in response to weather conditions,[66] and flexibly adjust their nesting behaviors in response to anthropogenic changes to their habitat.[68] Suitable nesting trees are critical resources for all chimpanzees,[60–62,64,66] and they tend to be selective of tree species and/or physical characteristics for nest construction, such as tree height and girth, branch pliability, and likely foliage density.[61,62,64,69–75]

It is assumed that the relatively low availability of tall trees, small proportion of closed vegetation, and predominance of deciduous vegetation contributes to a relatively low availability of suitable nesting trees and materials for savanna chimpanzees, especially during the dry season.[7,71,76,77] Following this hypothesis, the low availability of suitable nesting resources is a distinguishing challenge for savanna chimpanzees, except for conspecifics in highly deforested[68] or montane[78] landscapes where the availability of tall trees is also low. Although most closed vegetation types in savannas have relatively large trees with dense canopies, on average, they comprise a small proportion of the landscape. Savanna chimpanzees build their nests in closed and open vegetation types (e.g., Assirik,[76] Bagnomba,[77] Diaguiri,[73] Greater Mahale Ecosystem,[28,57,77,79] Fongoli,[80] Ishasha,[81] Semliki[64]). Deciduous trees in open vegetation types pose a challenge to nest building during the dry season because they lose their leaves. To address this challenge, chimpanzees in savannas may seasonally prefer to build nests in evergreen vegetation types due to the higher availability of leafy materials and, in open vegetation types, in deciduous trees that are flushed with new leaves during dry months.[28,65,76,82] Chimpanzees tend to select trees for nest construction that are relatively tall on the savanna landscape (e.g., Assirik,[76,83] Issa,[61,71] cf., Fongoli[83]). This preference for relatively tall trees may explain why there is some overlap in mean nesting tree and nest heights for savanna and forest chimpanzees (Table S4; Figure S1).[71] Furthermore, these overlapping means could be related to altitudinal effects[78,84] or topographic features (e.g., rocky areas)[85] that limit tree growth, and anthropogenic effects such as timber extraction.[27,83]Although more information is needed on the spatiotemporal availability of suitable trees and nesting materials across vegetation types to determine the extent to which savanna landscapes influence nest building behaviors, converging lines of evidence support the idea that nesting resources are relatively scarce.

4.2 | Food

The diets of savanna chimpanzees fit the species-wide patterns of ripe fruit specialization and flexible responses to local changes in food availability.[5,47,59,86–94] Savanna chimpanzees may experience variation in food availability that are intrinsically related to high rainfall seasonality.[7,89] For example, foods are expected to be less abundant and more widely dispersed in savannas,[4,7,45,46,89] because woody plant food availability is relatively low (e.g., Senegal)[26,95] and seasonal bushfires (e.g., Fongoli)[31]can prevent sapling growth.[34] Although savannas are hypothesized to produce lower food biomass relative to more forested landscapes due to the expected positive correlation between tree biomass and overall food biomass, these relationships are complex and rarely tested. In the only comparative study to date, it was found that food availability at the Fongoli savanna site was relatively low for all woody plant parts combined (e.g., leaves, flowers, and fruit) compared with the Taï forest site, but ripe fruit availability was unexpectedly higher at Fongoli.[95] This is a noteworthy finding because woody plant biomass comprises a lower proportion of vegetation cover on savanna landscapes. More cross-sectional and longitudinal ecological research is needed to identify the evolutionary processes and mechanisms that influence food availability along the savanna to forest continuum.

Except for Fongoli, where systematic direct observations of feeding and ingesting were possible,[27,87,96] savanna chimpanzee diet has been described by macroscopic fecal analysis, discarded feeding remnants, opportunistic direct observations, and stable isotope analysis.[5,46,47,90,97,98] Each of these indirect methods has its limitations. Foods that are easily digestible or indigestible but difficult to identify to the species level (e.g., herbaceous foods, insects lacking exoskeletons) are underrepresented with macroscopic fecal inspection.[90] Stable isotope analyses of carbon and nitrogen are informative for broad-level diet comparisons[98–100] but they are often not well suited for fine-scale dietary comparison (cf. Fahy et al.[101]), are confounded by physiological and other factors (e.g., Wolf et al.,[102] Oelze et al.[103]), often require a basic understanding of the isotopic context (e.g., Wessling et al.,[98] Oelze et al.[104]), and do not provide precise indications of quantity or presence of specific food in the absence of observational data. Thus, caution is warranted when interpreting dietary results from indirect methodologies. While direct observation of habituated study subjects produces high-quality dietary data, tall grasses may obscure visibility for observers, resulting in the underrepresentation of herbaceous plant foods in dense grass canopies. In spite of these methodological challenges, it is possible to identify distinctive trends in foraging and diet for chimpanzees in savanna landscapes.

Diets are relatively low in plant species richness (e.g., Assirik,[90] Fongoli,[92] Semliki,[36] Greater Mahale Ecosystem[5,47,97]) for savanna chimpanzees than for conspecifics in most forested landscapes (e.g., Lopé, Gabon,[47,105] cf. Nyungwe National Park, Rwanda,[106,107]). This trend is likely explained by the: (1) general pattern of lower woody plant species richness in savanna landscapes (e.g., West Africa)[108] and (2) tendency for these chimpanzees to ingest plant parts mostly from woody (not herbaceous) vegetation on landscapes dominated by grasses.[47,90,92] Assessing plant species richness effects on chimpanzee diets is needed because richness varies across savanna landscapes[14,26] and the contribution of herbaceous vegetation to diets in savanna landscapes is not well understood (see above). Given that many savanna unit-groups live outside of protected areas and crop-feeding occurs across the species' range,[10] domesticates may contribute to their diets. However, there is little evidence of crop-feeding in savanna chimpanzees to date (Box 2).

Chimpanzees in savanna landscapes extensively forage in woodland and forest vegetation types. Most of their plant foods are located in woodland vegetation.[5,27,47,89,92,98,109] At Issa, although six of the seven top plant foods only occurred in evergreen vegetation types, 61% of plant food species were located in woodland and chimpanzees intensified their use of this vegetation when forest fruit availability was low.[47]About 52% of plant foods at Assirik were located in woodland.[90] This study also reported that forests provided 29% of food species but comprised only 3% of the land area. The Issa and Assirik results are supported by time allocation studies at Fongoli, as these chimpanzees commonly fed in woodland but used forest for feeding more often than would be expected based on its availability (e.g., land cover).[27,30] The reliance on woodland for foraging is explained by its high land cover at savanna sites,[29,30] the relative abundance of woody plant foods,[110] and the occurrence of some highly productive fruiting tree species, such as *Adansonia digitata*,[111] in this vegetation type.

A growing body of evidence indicates that chimpanzees in savanna landscapes consume large amounts of non-fleshy fruit foods.[5,28,46,90,92,94] While all chimpanzees ingest a wide range of plant parts (e.g., fruits, flowers, pith, bark cambium, gum, leaves), the relative importance of each plant part varies among sites. For example, flower ingestion at Fongoli was much higher relative to sites in more forested landscapes in Tanzania (Mahale), Uganda (Budongo, Ngogo), and Republic of Congo (Goualougo) (reviewed by Watts et al.[94]). It is hypothesized that savanna chimpanzees ingest a higher variety of seeds and underground storage organs (USO) than chimpanzees in forests,[5,7,28,46,90] but inconsistent terminologies and categorization methods for fruits, seeds, USO, and roots limit what conclusions we can reach. In savanna landscapes, chimpanzees routinely ingest dry-adapted fruits (e.g., *Adansonia digitata*, *Thespesia garkeana*), pods (e.g. *Afzelia africana*, *Brachystegia* sp.), and seeds (e.g., *Jubernardia* sp., *Parkia biglobosa*), and it is hypothesized that such hard foods are difficult for them to process orally.[5,7,47,111,112] To test the idea that dry and hard foods are especially common for savanna chimpanzees, one study compared the elasticity and toughness of orally-processed foods at Ngogo and Issa.[113] The authors demonstrated that the dry-adapted plant foods at Issa, particularly fruits, were stiffer and tougher (Video S1). Additional research is needed to evaluate if and how variation in the physical properties of food exists across seasons and sites.

Chimpanzees rely on insect prey but its contribution to diets varies highly across communities. Insect ingestion frequencies for savanna chimpanzees are within the range of forest chimpanzee values (savanna range: 37.5%–60% of feces containing insects, forest range: 0%–88%).[114] At Fongoli, termites (*Macrotermes subhyalinus*) are a staple food because they are eaten throughout the year and ingested at a relatively high rate.[87] In contrast, termites are seasonally ingested at Assirik[115] and Issa,[116] and Semliki chimpanzees ignore them.[114] Inter-site variation in termite abundance[87] or handling time[114] offer explanations for flexible insectivory among savanna sites, but additional research on complementary explanations, such as balancing nutrients and meeting micronutrient requirements are needed, given that other food sources also vary across sites.

Converging lines of evidence indicate that savanna chimpanzees hunt and/or ingest meat less often than most unit-groups in forests,[117] including direct observations of hunting at Fongoli[95] stable isotope values of nitrogen from Senegal,[98] and macroscopic fecal inspection of undigested animal tissues at Issa.[117] These differences are a likely consequence of low prey availability in savannas.[46,117] The absence or scarcity of preferred prey at savanna sites, such as red colobus monkeys (*Piliocolobus* sp.),[118] may also be associated with the high frequency of hunting small prey, including bushbabies (*Galago* sp.), rodents, or lagomorphs.[117] At Fongoli, tool-assisted hunting for *G. senegalensis*, specifically, is concentrated during the rainy season,[96] and overlaps with months of fruit abundance and scarcity.[119] These patterns support the hypotheses that meat is seasonally important for some savanna chimpanzee populations,[117] and that tool use may be an adaptive response to environmental pressures[120] by way of necessity or opportunity (reviewed by Pruetz et al.[119]).

Open and dry landscapes may be a driver of extractive foraging innovations in some primate populations (e.g., white-fronted capuchins [*Cebus imitator*],[38] *Pan troglodytes*[7]) presumably because food and water are scarce at least seasonally and, in some cases, more difficult to obtain. Food seasonality is common across chimpanzee landscapes,[121] and savannas are no exception (Issa,[47] Fongoli[92,111]). At Fongoli[119] and Issa,[47] the rainy season is a time of plant food scarcity. Unlike more forested landscapes, annual bush fires and burn scars[31] affect tree availability,[34] which in turn affects the availability of foods produced by or found within trees (e.g., fruits, flowers, leaves, bark, gums, insect nests). There seems to be an association between seasonality and tool use for savanna chimpanzees to access embedded foods or water, such as hunting with spear-like tools,[96] time-intensive termite fishing,[87] digging for USOs with tools,[88] and water dipping with brush-tipped sticks.[122] Water dipping is closely associated with water scarcity at Comoé, Ivory Coast,[122] but relationships between seasonality and foraging tool use can be more complex. For example, tool-assisted hunting and termite fishing have seasonal peaks during the transitional and/or wet seasons at Fongoli but neither behavior can be simply attributed to fruit scarcity.[119] This lack of simple association between seasonality and foraging tool use might be due to multivariate causality in some cases.

Complex associations among seasonality, food availability, and extractive foraging are supported by research on chimpanzees in more forested landscapes. Food seasonality also occurs in more forested landscapes,[121,123] tool use innovations are widespread (e.g., nut-cracking, underground termite fishing, honey extraction, reviewed by Pruetz et al.[119] and Motes-Rodrigo et al.[124]), and some forest chimpanzees are known to allocate a significant proportion of foraging time to tool use (e.g., nut-cracking at Taï).[86] A cross-sectional study of food seasonality for savanna (Fongoli) and forest (Taï) chimpanzees found that the Taï forest landscape had higher seasonal variation of plant food and fruit (unripe and ripe combined) availabilities.[95] In addition, these authors reported that Taï chimpanzees displayed lower c-peptide values and higher C-peptide seasonality, indicating that these forest chimpanzees experienced more seasonally variable energetic balance than the Fongoli unit-group. This biomarker evidence supports the hypothesis that chimpanzees in savannas have effective behavioral strategies for coping with low (overall) food availability.[101–121,123] Additional research is needed to understand the relationships between food availability and behavioral adaptations (e.g., foraging tool use) that hypothetically maximize or balance nutrient and energy intakes through opportunistic food encounters and/or minimize nutritional or energetic shortfalls during periods of food scarcity.

4.3 | Water

The hot, dry, and seasonal environments that savanna chimpanzees experience influence water availability, water intake (input), and water loss (output) through metabolic processes. Sources of water inputs include metabolic water, surface water, and preformed water.[125,126] Inputs from surface water will be the focus of this section, as there is a lack of information on preformed and metabolic water inputs for chimpanzees. Water output results from micturition, respiration, defecation, and insensible perspiration.[126] Additional water loss occurs in hot temperatures from evaporative cooling (i.e., sweating) and panting.[126–129] While chimpanzees in more forested landscapes drink surface water and may experience dehydration risk,[123,130] surface water is predictably scarce for many savanna unit-groups during the dry season.[7,29,30] At Fongoli, individuals drink water almost daily (Box 2)[27] and routinely show physiological indications of dehydration.[123] This persistent state of dehydration may have led to behavioral adjustments that help to maintain water balance.[95]

Permanent water sources may also influence ranging behavior and choice of food patches or sleeping locations. In Senegal, savanna chimpanzees appear to range close to permanent water sources during the dry season and may intensify foraging for food here, depleting these areas at a faster rate.[30,45] In support of this hypothesis, individuals ingested more fruit at feeding trees located closer to water sources, controlling for variation in food quality.[27] During the dry season, chimpanzees in the Greater Mahale Ecosystem often construct their nests closer to permanent water,[77] but they can also nest far from these sources, suggesting that proximity to water may not always limit their range.[28]

Chimpanzees may use tools or manipulate surface substrates to gain access to drinking water. For example, although savanna and forest chimpanzees are known to use tools or hands to drink from surface water in tree cavities, chimpanzees in the savannas at Comoé more commonly use water-dipping sticks during the dry season.[122] Digging shallow wells, 5–15 cm deep, by hand has been observed at Assirik (Video S2), Greater Mahale Ecosystem (Ndimuligo and Hernandez-Aguilar, unpublished data), Fongoli (Pruetz, unpublished data), and Semliki.[46,131] Well digging likely increases access to surface water overall,[131] but chimpanzees also dig wells near flowing water, perhaps to access cleaner or better-tasting water.[46,132]

4.4 | Temperature

Microclimates with ambient temperatures lower than the body temperature of chimpanzees can be scarce in savannas.[133,134] There is high variation in average and maximum temperatures across chimpanzee sites, with East African and lower latitude West African savannas exhibiting temperature conditions that largely overlap with those of more forested sites.[11,123] Although mean annual temperature across all chimpanzee sites is below the body temperature threshold, it is ~2°C higher at savanna sites, overall.[11] Moreover, in high latitude West African savannas in Senegal and Mali, the mean maximum daily temperature is about 2°C higher than body temperature, and daily maximums may routinely exceed 40°C.[29,30,95,134,135] Very little is understood about physiological adaptation and acclimation to hot climates for chimpanzees in general, but they respond to heat stress through sweating and panting,[133] and have a relatively high ratio of eccrine to apocrine glands (2:1) relative to most other nonhuman primates.[127] In savanna environments, high temperatures might work synergistically with low water availability to accentuate simultaneous risks of dehydration and hyperthermia.[95,136,137] Evidence of this challenge is displayed in chimpanzees at Fongoli, who have higher urinary cortisol levels, a biomarker of physiological challenges, during the hottest and driest months of the year.[95]

At Fongoli, the behavioral responses of chimpanzees to hot and dry conditions are thoroughly documented. These individuals employ two behavioral strategies to prevent hyperthermia; first, they minimize exertion during very hot conditions and second, they extensively use cooler microclimates within their home range.[30] The long periods of inactivity displayed by chimpanzees at Fongoli during the hottest hours of the day are more than double the average length for chimpanzees overall,[30] and likely minimize the risk of exertional heat exhaustion or stroke.[138] The microclimate of the forest understory can be several degrees cooler than nearby open vegetation types within savanna landscapes.[139] Fongoli chimpanzees preferentially use forest vegetation for resting, socializing, drinking, and nesting.[30] While feeding in woodland and grassland, they likely minimize UV-radiation exposure as evidenced by higher rates of fruit ingestion in these vegetation types after controlling for macronutrient and energy concentrations in their foods.[27] In the early wet season at Fongoli, when temperature and humidity are high, chimpanzees routinely submerge the lower portions of their bodies in shallow pools of water while drinking and soaking.[30] Savanna chimpanzees seek refuge from soaring dry season temperatures in caves and rock shelters in Mali (Bafing: J. Moore, personal communication) and Senegal (Study sites: Bagnomba,[85] Dindefelo,[140] Drambos,[141] Fongoli[134]). Finally, chimpanzees in savannas appear to allocate time to feeding, traveling, drinking, bathing, and socializing activities during the night, when temperatures are lower.[142,143] Savanna chimpanzees in the Greater Mahale Ecosystem may form larger parties at night than during the day,[7,79] which could also favor nocturnal socialization but data from habituated chimpanzees are needed to confirm this hypothesis. Nocturnal activity occurs in chimpanzees across their range, but a relatively high frequency appears to distinguish savanna chimpanzees from most forest conspecifics.[142,143] Seasonal differences in nocturnality have been reported for Fongoli,[142] but it is unknown if these also exist in more forested sites. These behavioral adjustments underscore the importance of behavioral flexibility to savanna populations living in extremely hot climates, but the seasonally-elevated cortisol levels found in Fongoli chimpanzees hints at limits to their thermoregulatory tolerance (Box 2).[123]

5 | POPULATION DENSITIES, SOURCES, AND SINKS

Savanna chimpanzees live at lower population densities and range over larger areas relative to conspecifics in more forested areas (Table S1). It is hypothesized that this is due to the low carrying capacity of savanna landscapes resulting from their characteristic low abundance or scattered distribution of foods (cf. Wessling et al.[95]) and water. In addition to differences in vegetation, there are many ecological reasons (e.g., elevation, food availability) for differences in chimpanzee population densities.[26,56,144–148] These factors are not mutually exclusive. Chimpanzees in savannas tend to have larger community home ranges (savanna range: 85–90 km^2, $N = 2$; forest median [range]: 13 [3–30] km^2, $N = 26$) and lower population densities (savanna median [range]: 0.09 [<0.01–12.5] individuals/km^2, $N = 29$; forest median [range]: 1.9 [0.39–9.2] individuals/km^2, $N = 31$) than chimpanzees in more forested landscapes (Table S1). Note that there is a wide range of density estimates from different methods among studies (Table S1), and from varying kinds and degrees of anthropogenic activities that may or may not exhibit diachronic change.[56,144,146,149]

Lower population densities on savannas are somewhat consistent with the ideas that *P. troglodytes* is a forest-adapted or forest-suited species[150,151] and that savanna chimpanzees represent population sinks that are supported by immigrants from forest-population sources.[150–152] A problem with this logic, however, is that population density comparisons alone are insufficient for identifying sources and sinks.[153–155] Testing the forest/source-savanna/sink hypothesis requires known birth, death, and migration rates (or genetic proxies) among chimpanzees in savanna and more forested landscapes, as these life-history traits are not always concordant with population size or density.[155]

6 | CHIMPANZEE SOCIETIES IN SAVANNA LANDSCAPES

Savanna chimpanzees exhibit a mosaic of fixed and labile social behaviors that are likely related to phylogenetic constraints and behavioral flexibility. Savanna chimpanzee dispersal patterns and hierarchical structures conform to the species typical patterns of male philopatry and dominance.[156,157] All chimpanzee societies have social structures comprised of a multi-female and multi-male unit-group or community that flexibly fissions and fuses into unit-subgroups or parties in response to ecological or social factors (hereafter, we use unit-subgroup and party interchangeably).[158,159] Relative to many chimpanzee communities in more forested areas, reports from several savanna chimpanzee sites suggest that unit-groups can be highly cohesive. Sporadic observations of unhabituated chimpanzees ranging in large parties, including females and males of all ages, at Assirik[160] and in the Greater Mahale Ecosystem[89,161] are supported by observations of habituated chimpanzees at Fongoli.[30] Research at Fongoli shows that all or most community members are seen together within a single day, and that unit-subgroup sizes are larger during the wet season compared with the dry season.[30] This study also compared unit-subgroup size at Fongoli to those from more forested areas and found that Fongoli chimpanzees exhibited the highest absolute and relative (adjusted for unit-group size) averages. Within-community social behavior at Fongoli is similar to that reported for chimpanzees elsewhere, but the community also appears to be characterized by high levels of social tolerance, where adult males allow adult females to take food and feeding locations from them.[162] Counter to the hypothesis that greater cohesion and integration among males and females is driven by the savanna landscape, western chimpanzees (*P. t. verus*) in forest landscapes also exhibit strong mixed-sex sub-grouping patterns (Taï).[163] Direct observations of habituated Issa chimpanzees (Box 1) on community and party ranging will be particularly important for evaluating landscape or subspecies hypotheses for social cohesion because indirect methods for investigating social organization and structure for unhabituated chimpanzees (e.g., camera traps, nest counts) are noisy.[164]

How savanna chimpanzees maintain their expansive community home ranges while living at low densities remains largely unknown but early evidence indicates that community defense behaviors are diverse. Typically, chimpanzee males defend community home ranges through boundary patrols.[165–168] Lethal inter-community aggression is an extreme form of group defense that widely occurs in chimpanzees but is more common in the eastern subspecies (*P. t. schweinfurthii*).[167,169] At Fongoli, boundary patrolling near an adjacent community's home range has never been observed during 15 years of systematic behavior sampling, though excursions of large mixed-sex parties from the Fongoli community into the neighboring community's home range, along with vocal battles between these two unit-groups have been recorded several times (Pruetz, unpublished data). Although all male parties in the Greater Mahale Ecosystem were rarely recorded during opportunistic observations of unhabituated chimpanzees,[5,170] new data from habituated individuals at Issa (Box 1) show that such parties occur, and an inter-community killing has been observed in this context (Piel and Stewart, unpublished data). Furthermore, chimpanzee parties have changed behavior in areas of community ranging overlap, in ways consistent with descriptions of patrolling behavior (e.g., non-vocalizing rapid travel). However, mixed-sex parties have also been observed in these areas (Piel and Stewart, unpublished data). Explaining why community home range defense at Issa contrasts with Fongoli will require additional research.

7 | SIGNIFICANCE TO HUMAN EVOLUTION

The study of savanna chimpanzees sheds light on the adaptations of great apes to highly seasonal, dry, hot, and open landscapes. Comparisons of behavior, morphology, and ecology between savanna chimpanzees and conspecifics living in more forested landscapes provide a "testing ground" for theories of how early hominins may have adapted as African forests were retreating millions of years ago.[5,7,29,30,99,171] This does not suggest that chimpanzees are present-day equivalents of early hominins (e.g., *Ardipithecus ramidus*, *Australopithecus anamensis*) and we recognize that there are some limitations to using chimpanzees as models for hominin evolution.[1,7,172] Understanding the selection pressures that shaped human evolution starts with an examination of hominin fossils. Despite a robust hominin fossil record that dates back to the late Miocene[173–176] and an archeological one to the early Pliocene in East Africa,[177–179] little is known about the behavioral adaptations of early hominins as they transitioned from a relatively more arboreal lifestyle and wet climate to terrestrial and dry conditions. Although the extent of similarities and differences in morphology and behavior between the LCA of *Pan* and *Homo* and its descendants is contested,[172,176,180–182] hominin evolution was likely tied closely to adaptations to dry, open, and seasonal environments.[3,183] As a result, chimpanzees that live in savanna landscapes are used as models for investigating this transition (Box 1).[1,30,89] Specifically, chimpanzees that inhabit analogously similar environments to those reconstructed for some hominin species[2,184–186] hold the potential to inform hypotheses on ecologically-driven adaptations absent in any fossil deposit.

Hominin environments during the Pliocene involved complex landscapes that varied across time and space. Environmental reconstructions based on analyses of fossils, isotopes, and geological contexts from some early hominin deposits include, among others, a wide variety of savanna landscapes. For the early Pliocene hominin *Ardipithecus ramidus*, these reconstructed landscapes included a mosaic of vegetation types with forest, woodland, grassland, and floodplains.[2,186–190] For *Australopithecus anamensis*, reconstructed savannas included miombo woodlands and mosaic landscapes with woodland, grassland, and some forest.[191–196] Savanna landscapes for *Au. afarensis* included a variety of mosaic landscapes ranging from a mix of open woodland and grassland vegetation types to a combination of woodland, grassland, floodplain, and riparian forest vegetation.[191,197–200] A mixture of grassy and woody vegetation types characterized the landscape for *Au. sediba*.[201] This variability in hominin environmental reconstructions matches that of contemporary savanna chimpanzee sites, each of which may serve as an appropriate model for a particular paleolandscape.

The ecological continuity between contemporary savanna sites likely reflects a similar continuity over time,[189,202,203] (but see Faith et al.[204]). We can thus test hypotheses that address the selective forces that may have acted upon extinct hominins.[198,205] Hypothesis testing often centers on diet, locomotion, and positional behavior with intense scrutiny paid to selection pressures that potentially triggered the evolution of bipedalism.[206–209] Dental biomechanical,[210] isotope,[211] and microwear[212] approaches provide independent measures of hominin diet, and these methods also advance analyses of extant ape cranial morphology and diet in savanna landscapes, such as the physical properties of foods[113] and the relative importance of C_3 and C_4 foods.[99]

Comparisons of savanna and forest chimpanzees demonstrate the utility of referential models for reconstructing early hominin diets. Carbon stable isotope ($\delta^{13}C$) values differentiate feeding strategies that focus on woody (C_3) or grassy (C_4) plants. While relatively high $\delta^{13}C$ values for many early hominins provide solid evidence of feeding on C_4 vegetation in open landscapes, and chimpanzees in forest landscapes have lower $\delta^{13}C$ values that are consistent with feeding primarily on woody plants, carbon isotope values for savanna chimpanzees and some early hominins, including *Ar. ramidus*, *Au. anamensis*, and *Au. sediba*, are more similar to each other than to any other early hominin or forest chimpanzee.[213,214] These findings are consistent with the idea that some early hominins inhabiting savanna landscapes primarily ingested C_3 plants, similar to what is known about the diets of savanna chimpanzees. These referential models enable us to test the long-established hypothesis that savanna environments promoted hunting and meat consumption in the earliest hominins.[215] Counter to this hypothesis, a study comparing savanna and forest chimpanzee meat ingestion found evidence to the contrary: savanna chimpanzees probably eat less meat than most forest conspecifics.[117] As this study did not support the meat-eating hypothesis, the results compel us to carefully re-evaluate long-held assumptions about the ecological determinants of behavior.

Questions concerning behavior-environment relationships have implications for how we model hominin adaptations to changing environments during the Pliocene and Pleistocene.[81,216,217] In savanna landscapes where resources were presumably widely scattered and less abundant, early hominins may have experienced trade-offs among sociality, resource competition, and locomotor efficiency.[207,218] Under these conditions, hind limb adaptations for bipedal walking may have evolved to increase energy efficiency.[218] For hominids that retained quadrupedalism on savanna landscapes, changes in social structure, such as decreasing social group sizes, may have been advantageous.[207] Alternatively, bipedalism may have increased foraging efficiency in savanna landscapes through increasing ingestion rates while feeding on fruits from shrubs and small trees (i.e., the postural feeding hypothesis).[206] In support of this hypothesis, evidence from Semliki suggests that chimpanzee femora and pelves are more hominin-like than those of chimpanzees in more forested areas,[132] but a larger sample size from Semliki and other savanna chimpanzee sites is needed to reinforce this claim. The above and related questions are testable by observing extant ape behavior during times of food and water scarcity, investigating subsequent behavioral and physiological responses,[30,95,123] and comparing kinematics and kinetics among wild and captive apes to evaluate how substrate use and ranging behavior differ for chimpanzees confronting different environments.[219–221] Such data will demonstrate not only how chimpanzees negotiate open landscapes, but also how anatomical signatures may be useful in reconstructing fossil hominin locomotion.[222]

8 | CONCLUSIONS AND RECOMMENDATIONS

Climate, hydrology, geomorphology, topography, soils, fire, herbivory, and human activities interact to form savanna landscapes that chimpanzees occupy across the African continent. Our review summarizes evidence indicating that the environmental conditions of savanna landscapes can trigger behavioral, cultural, morphological, or physiological responses in chimpanzees. We term this process the "savanna landscape effect."

Savanna landscape effects appear to operate at global, regional, and local scales. Low population densities and large home ranges for savanna chimpanzees are the most pervasive pattern of the savanna landscape effect, globally, confirming observations of early savanna chimpanzee researchers (Box 1). In addition, behaviors such as digging shallow wells by hand may be common (but see Lapuente et al.[122]), but more research is needed to evaluate prevalence across sites. Traits associated with the savanna landscape effect may occur regionally or locally due to variation in culture and/or environmental conditions among landscapes. For example, cave use is prevalent in the hottest and driest region within the chimpanzee distribution, but has not been observed in savanna landscapes where average maximum temperatures are lower. Our ability to fully evaluate the savanna landscape effect is constrained by the small number of savanna study sites (Box 1). Cross-sectional research is needed to test for local effects when the candidate behavior is confirmed for only one unit-group, such as soaking in pools of water (Fongoli) or ingesting hard foods (Issa), for regional effects such as cave use, and to determine global savanna landscape effects. Due to more detailed studies on behavioral diversity and environmental conditions since the earliest savanna chimpanzee research (Box 1), there has been an increased awareness that savanna landscapes are not universally more harsh and extreme than more forested areas. For example, environmental pressures such as food and water scarcity may also occur in more forested areas and savannas can be periodically plentiful.[94,130] Therefore, we recommend that future studies use caution while making generalizations about savanna landscapes. Nevertheless, this synthesis identifies continental and regional patterns of savanna landscape effects and shows that hot, dry, and open landscapes produce complex environmental conditions that can be distinct from more forested areas. Now, we need to identify the causal mechanisms of each savanna landscape effect.

To move the field forward, it is essential to more fully understand the diversity of savanna landscapes that chimpanzees inhabit. Future advances on this front are expected from looking at the landscape as a continuous set of environmental variables. While all abiotic and biotic factors on savanna landscapes might directly or indirectly contribute to the savanna landscape effect, traditional savanna chimpanzee research mainly focused on climate factors and vegetation cover to explain behavior-environment relationships, specifically high rainfall seasonality, low annual rainfall, high temperatures, and percentages of open and closed vegetation types.[4,7,29] We recommend that researchers move towards a more comprehensive understanding of savanna landscapes, starting with interdisciplinary, comparative research on the conditions of savanna and forest study sites. This will require descriptions of surface water availability, edaphic conditions, fire regimes, herbivory, and predator–prey interactions, in addition to climate, land cover, vegetation types, and food availability. The publication of geographic coordinates that are representative of the study site will be important for research integrating remotely sensed data.

In addition to understanding the diversity of savanna landscapes, longitudinal and cross-sectional research on behavioral variation corresponding to this diversity will inform our understanding about the relationships between behavioral diversity and environmental variability. The savanna landscape effect might operate through adaptation, acclimation, behavioral or ecological flexibility, or some combination of these mechanisms for each trait of interest. Moreover, the savanna landscape effect is not mutually exclusive with other processes that produce behavioral diversity, such as culture.[223] Intraspecific, comparative research in chimpanzees has shed light on the role of the savanna landscape effect as a driver of behavioral diversity,[224] but more work is needed to disentangle the savanna landscape effects from more general environmental variability. Nonetheless, this research suggests that savanna landscapes are likely to promote behavioral diversification.

Our synthesis of savanna chimpanzees provides exciting material for such mechanistic research. Novel and cutting-edge research on the savanna landscape effect will benefit from interdisciplinary approaches and granular measures of behavior, anatomy, physiology, and resource availability (i.e., abundance and distribution). Behavioral studies on the savanna landscape effect could concentrate on mechanisms of social cohesion using tools such as social network analysis to understand how unit-groups maintain social bonds within large home ranges and at low population densities. Adaptation research involving water scarcity and hyperthermia risk will benefit from evaluations of heat-shock proteins and the ecomorphology of kidneys, sweat glands, and hair filaments in chimpanzees and closely related species across diverse landscapes. Traditional methods for measuring the availability of nesting trees and materials, food, water, and cool microclimates are important but provide only gross estimates of the environmental conditions that affect chimpanzees in real time. For instance, our review of nesting resources shows an underlying gap in inter- and intra-site estimates of nest tree density and distribution for chimpanzees along the savanna to forest continuum (Table S4, Figure S1). Thus, the claim that nesting tree availability is lower in savanna landscapes relative to more forested areas remains speculative.

While our evaluation of savanna landscapes mostly confirms widespread views about resource scarcity, there are exceptions. That compared with Fongoli, Taï chimpanzees were found to vary more seasonally in their C-peptide levels while inhabiting an environment with measurably lower and more variable ripe fruit availability[95] demonstrates that resource availability is more nuanced, in some cases at least, than can be deduced from simple comparisons of woody biomass across forest and savanna landscapes. Increased scrutiny needs to be paid to the common assumption that food is scarcer for individuals on savanna landscapes through cross-sectional studies of food biomass, phenology, and macronutrient concentrations. Furthermore, if a pattern of higher food availability in savanna landscapes is confirmed with further research, there is a need to identify which factors, other than food, lead to the lower population carrying capacity in savanna landscapes relative to more forested areas.

In the future, inter-specific comparative research will be instructive to adaptive scenarios for the savanna landscape effect. Phylogenetic comparisons among sympatric and closely related species (Table S3) have the potential to identify homologous and analogous traits, and tease apart adaptation from closely related mechanisms, such as acclimation and behavioral flexibility. Savanna landscape effect patterns are reported in a variety of nonhuman primate populations in open and dry environments, where populations are known to flexibly (e.g., savanna baboons [*Papio cynocephalus*],[37] vervet monkeys [*Chlorocebus pygerythrus*],[40] white-fronted capuchins[38]) or adaptively (e.g., lemurs),[39] respond to resource scarcity. Although an intensive comparison of chimpanzees and bonobos (*Pan paniscus*) is beyond the scope of this review, it will be important to identify how and why bonobos seem to be more geographically limited by forest cover than their sister species. Recent advances in evolutionary theory, such as the extended evolutionary synthesis,[225] lead us to the conclusion that processes underlying savanna landscape effect patterns will be complex and numerous. That said, this comparative approach is a step forward in identifying the evolutionary pathways of savanna landscape effect traits in chimpanzees and other primates.

The question of what makes savanna chimpanzees different from conspecifics in more forested landscapes has captured the interest of researchers and broader society because of their comparative significance to human origins. The savanna landscape effect is a predicted driver of several adaptations in early hominins, such as bipedality, brain expansion, and cumulative culture (seasonality hypothesis,[3] savanna hypothesis[1]). As demonstrated here, the continued use of chimpanzee models has great potential to advance key topics in human origins research, such as positional and locomotion behavior and thermal tolerance.

For future research on savanna chimpanzees, as for any type of research, we highlight the importance of inclusivity, social justice, and environmental sustainability to research programs.[226] In recent years, there has been an increased awareness that traditional studies sponsored by research institutions in the United States, Canada, and European Union, have historically neglected Japanese contributions to primatology,[10] and may have contributed (knowingly or unknowingly) to extractive (neocolonial) research systems.[227–230] The reasons underlying such inequities are multiple and complex; however, it is also the case that chimpanzee field sites have employed local staff, worked with range country scientists at universities, coordinated with wildlife departments, and increasingly made outreach with local communities a priority (e.g., Wrangham and Ross[226]). Building on that legacy, researchers can support inclusive, range-country programs with fully engaged and equitable partnerships involving diverse leadership and representation from African scholars, practitioners, and institutions.[226] These relationships can be leveraged to build research capacity (e.g., research facilities), professional development programs, student training opportunities, provide assistance for job placement, and support community service projects.

As discussed in Box 2, understanding the savanna landscape effect in chimpanzees is critical for improving our ability to protect and manage populations from endangered or critically endangered (sub)species. In the immediate future, conservation research needs to concentrate on ground-truthing critical resources (e.g., permanent water sources), examining genetic continuity among savanna chimpanzee unit-groups, and evaluating human cultural aspects of land use with mixed methods approaches such as ethnoprimatology.[56] Generating such information will allow practitioners to build better national or regional habitat suitability models and identify biological corridors on landscapes for protection. In addition, the increasing awareness of the ethical issues of fieldwork, such as zoonotic disease transmission and vulnerability for habituated study subjects, makes the inclusion of scientifically sound best practice guidelines essential to wild chimpanzee field programs.[231–233] The COVID-19 pandemic further illustrates the urgent need to practice disease transmission prevention during fieldwork.[234] The integration of inclusive savanna chimpanzee research and conservation, as described above, will hopefully contribute to fruitful collaborations with diverse stakeholders representing a wide range of economic and political interests, wherein primatologists directly or by proxy are more likely to be heard during national and international policy discussions on sustainable development in chimpanzee range countries. In sum, we anticipate a vibrant future for savanna chimpanzee research and hope that our recommendations help to guide future studies.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

GLOSSARY

C_4 grasses: C_4 grasses get their name from the four-carbon molecule they produce through fixation of atmospheric carbon dioxide. C_4 photosynthesis is more efficient than the ancestral C_3 form (only three-carbon molecule), and widely believed to be an adaptation to hot and open environments. As such, C_4 grasses are widespread in tropical savannas.

Closed vegetation: Types of vegetation characterized by a dense canopy cover, usually at the height of the tree canopy, which effectively blocks most sunlight from reaching the ground and creates a shaded understory. Examples of closed vegetation types used by savanna chimpanzees include gallery/riparian forest and dense bamboo woodland.

Deciduous (tropical vegetation): Plants in the seasonal tropics that shed their leaves and/or die during the dry season, in most cases. Perennial plants shed their leaves and conserve water and nutrients in underground storage organs or roots until the rains return. In annual plants, individuals usually die soon after seed dispersal.

Ecotone: A transitional zone characterized by two or more vegetation types that intertwine within a single area, such as a place where forest and grassland converge.

Environment: The exosomatic and physical surroundings that an individual experiences.

Evergreen (tropical vegetation): Plants in the tropics that retain their green leaves throughout the year.

Forest: Vegetation type with dense stands of trees and lianas that collectively form a connected forest canopy. Forests can be semi-deciduous or evergreen, or a mixture of both. See "Woodland" for a description of tropical dry forests.

Gallery/riparian forest: Typically evergreen forests that occur along rivers and permanent or seasonal streams.

Grassland: Vegetation type in open areas that are characterized by C_4 grasses, sedges, forbs, rushes, and less than 10% shrub or tree cover.

Greater mahale ecosystem: A vast area of predominantly miombo woodland east of Lake Tanganyika and south of the Malagarasi River in Tanzania. It encompasses regions termed Ugalla and Masito in the primatological literature. The historic and current savanna chimpanzee study sites of Kasakati, Filabanga, Nguye, and Issa are located here.

Habituation: The process by which wild animals, such as chimpanzees, become tolerant to the presence and close proximity of human observers. Habituation is a key method of primatologists to acquire quantitative and systematic measurements of behavior.

Hominid: All extinct and extant members of the Family Hominidae, also known as great apes, that includes four living genera: *Homo*, *Pan*, *Gorilla* and *Pongo*.

Hominin: Habitual or obligatory bipedal members of Family Hominidae, also known as the human clade that split from the panins (Genus *Pan*).

Hyperthermia: A potentially lethal condition wherein body temperature exceeds the critical threshold for intrinsic cooling mechanisms to function properly.

Land cover: The relative amount of area on a landscape that is comprised of specific vegetation types or major features (e.g., settlement, cropland, road, lake).

Landscape: A merging of ecology and geography, where physical structures (e.g., vegetation cover, corridors, watersheds, croplands), as well as abiotic and biotic components of an ecosystem function (e.g., patch dynamics, animal movement) occur within a spatially defined area. The scale of a landscape is calibrated to the species of interest, oftentimes, but not always, at the level of individuals and/or groups. For instance, a leaf miner's landscape will be much smaller than a baboon's. In general terms, a landscape is larger than an individual's home range or territory, but smaller than its species or subspecies geographic distribution.

Miombo woodland: Vegetation type principally consisting of deciduous trees from the Leguminosae family, including genera *Brachystegia*, *Isoberlinia*, and *Julbernardia*. Miombo woodland is found in southern, central, and eastern Africa. Mature miombo trees reach heights of 15 to 20 m.

Mosaic: The patchy spatial arrangement of numerous vegetation types on a landscape. For example, a savanna mosaic may describe a predominantly open patchwork of woodland, forest, and ecotone vegetation types within an area.

Open vegetation: Types of vegetation characterized by an open tree canopy that allows sunlight to reach the ground, as evidenced by the nearly continuous layer of C_4 grasses. Examples of open vegetation types used by savanna chimpanzees include woodland, wooded grassland, and grassland.

Preformed water: H_2O in the extracellular and intracellular spaces of organismal tissues.

Referential model: An organism that functions as a necessarily reductive replacement for another organism during hypothesis testing. Such model organisms function as representatives for species that cannot be used in research for ethical or logistical reasons. In evolutionary anthropology, extant primates serve as model organisms for extinct primates and fossil hominins especially, by way of evolutionary analogy or homology.

Savanna: Mixed tree-grass systems primarily consisting of fire-adapted trees and C_4 grasses at the landscape scale.

Soil fertility: Within the soil horizons, the relative concentration of nutrients available for plants to uptake.

Study site: A place where short or long-term field research is or has been performed. In practice, site investigators typically, but not always, define the geo-spatial boundaries and areas of these places.

Unit-group (community): A larger unit of social organization for fission-fusion species like chimpanzees. A unit-group consists of females and males of all age classes, and all individuals within this unit share membership to this group. Emigrants must be accepted by a critical mass of community members. In daily life, this group frequently "fissions" into smaller social units called unit-subgroups or parties. Although there are many determinants of group cohesion, fusion often occurs when food availability is high or one or more females are in estrus.

Unit-subgroup (party): A smaller unit of social organization for fission-fusion species. A subgroup consists of one or more individuals from a single community. Parties may consist of females and their offspring only, males only, or some combination of females and males from any age class. Subgroups temporarily fission from the larger community and may change composition several times during the day. Fissioning is mainly thought to reduce within-group feeding competition.

Vegetation types: Plant assemblages that are adapted to the abiotic and biotic conditions of particular areas within a landscape, such as grassland, woodland, forest, and ecotone.

Wooded grassland: Vegetation type characterized by open areas that includes C_4 grasses, sedges, forbs, rushes, shrubs, and 10%–40% shrub or tree cover.

Woodland: Vegetation type with stands of mostly deciduous trees and lianas with 40% or more tree cover. Open woodlands have fewer trees and a more continuous layer of C_4 grasses or bamboo, a C_3 grass, while forbs and vines tend to characterize the understory of closed woodlands during the wet season due to the higher shade cover. In tropical savanna landscapes, all woodlands are open during the dry season after leaf senescence. Tropical dry forest is functionally and structurally similar to woodland.

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SUPPORTING INFORMATION

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