

Annual Review of Environment and Resources African Environmental Change from the Pleistocene to the Anthropocene

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Africa, environmental change, climate, agriculture, megafauna, colonialism

Abstract

This review explores what past environmental change in Africa—and African people's response to it—can teach us about how to cope with life in the Anthropocene. Organized around four drivers of change—climate; agriculture and pastoralism; megafauna; and imperialism, colonialism, and capitalism (ICC)—our review zooms in on key regions and debates, including desertification; rangeland degradation; megafauna loss; and land grabbing. Multiscale climate change is a recurring theme in the continent's history, interacting with increasingly intense human activities from several million years onward, leading to oscillating, contingent environmental changes and societally adaptive responses. With high levels of poverty, fast population growth, and potentially dramatic impacts expected from future climate change, Africa is emblematic of the kinds of social and ecological precariousness many fear will characterize the future globally. African people's innovation and adaptation to contingency may place them among the avantgarde with respect to thinking about Anthropocene conditions, strategies, and possibilities.

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1. INTRODUCTION

How might understanding past environmental change in Africa—and the strategies adopted by Africans to deal with it—shed light on how to contend with future environmental changes on the continent and beyond? That question drives this review, setting the terms for our spatial and temporal frame, as well as our interdisciplinary focus. Recent proposals to establish a new geologic epoch to follow the Holocene—called the Anthropocene—have thrust into view the importance of understanding how humans drive and negotiate environmental change. As the site of human origins, the continent of Africa potentially has much to tell us about the ways that environmental changes have articulated with human evolution, ecology, and society. Oscillating environmental changes are at the center of the human story in Africa over evolutionary and historical time. The Anthropocene epoch is thus not the first time that humans, and other species, have encountered abrupt environmental change. With a better understanding of the ramifications of such changes, as well as their long-term legacies in social and ecological formations, African environmental histories could serve as important tools for predicting and preparing for future global change, even as the uniqueness of Anthropocene conditions imposes limits on the applicability of those tools. Moreover, Africa is emblematic of the kinds of precariousness many fear will increasingly characterize social and ecological systems across the globe, with high levels of poverty, fast population growth, and dramatic impending climate-change impacts. That precariousness has often been described as a symptom of African ineptitude, and the continent has long been considered to be "lacking," "marginal," "dysfunctional," or trapped by "tradition" (see 1). But recent work in social theory (e.g., 2-5) has shown that, in fact, Africa is a place of incredible innovation in the face of contingency and adversity, a place where novel social and ecological arrangements are forged. As such, Africa stands at the forefront of thinking about Anthropocene conditions, strategies, and possibilities.

Our review builds on these insights, presenting the latest understanding on the nature, drivers, and consequences of environmental change in Africa's ecosystems. Because such systems today are products of culture and power as much as temperature and rainfall, our approach is anchored

Holocene: the epoch occurring 11,700 BCE-1945 CE, distinguished by the global spread of modern humans and their ecosystem effects through agriculture, pastoralism, fire, and hunting; climatic variability within the Holocene is muted relative to the Pleistocene but still with substantial environmental impact

in both social and ecological theory. Our temporal focus traverses the Pleistocene, Holocene, and Anthropocene, the period spanning early stages of hominin evolution, the origin of anatomically modern humans, and that species' partial transformation of the natural world (6). But humans are not the sole shapers of environments—nor are humans an undifferentiated mass—so our analysis includes the effects of climate, nonhuman organisms, and attention to how different groups of humans impact environments. Specifically, we focus on four drivers of change, chosen due to their prominence in the literature, their overall influence in environmental transformation at broad scales, their illustration of the diversity of processes encapsulated by the term environmental change, and the serious challenges they pose to conservation and adaptation today: (a) climate; (b) agriculture and pastoralism; (c) megafauna; and (d) imperialism, colonialism, and capitalism (ICC). These drivers sometimes overlap and operate at distinct spatiotemporal scales (see Figure 1). Our review spans the Sahara, commonly used to divide Africa geographically but livable during multiple periods of the Pleistocene and Holocene; however, we do not cover Madagascar nor other islands where ecological and evolutionary histories are shaped by the particularities of island ecosystems.

Describing environmental change across these spatiotemporal scales requires attention to both broad trends and specific cases. Accordingly, for each driver of change we review, we zoom in

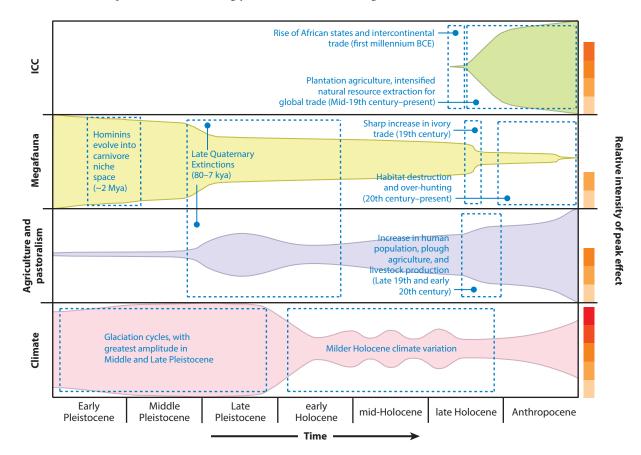


Figure 1

Depiction of the changing intensity over time of the four drivers discussed in our review. Orange/red bars on right describe the intensity of each driver at the period of highest effect, relative to other drivers. Abbreviation: ICC, imperialism, colonialism, and capitalism.

Anthropocene: the epoch occurring 1945 CE-Present, which is not yet formally added by geologic commissions given debates regarding adequate stratigraphic signatures, optimal boundary dates, and the possibility of naming an epoch in media res; we follow Zalasiewicz et al. (6) in suggesting that the clearest rationale for the onset date is the mid-twentieth century, inaugurated by nuclear testing producing a global radionuclide signal, rapid increase in greenhouse gas emissions, and a trend toward strong human impact on Earth's biosphere and atmosphere

Pleistocene: the epoch occurring 2.588 Mya-11,700 BCE marked by repeated glacial-interglacial changes that manifested in Africa as alternating arid-cool and humid-warm phases; the Late Pleistocene saw the Last Glacial Maximum (\sim 21 kya) and a subsequent warming interrupted by a cooling period known as the Younger Dryas (12,900-11,700 ya); across the Pliocene-Pleistocene boundary, the genus Homo emerges

on a specific case: respectively, desertification in the Sahel-Sahara zone, rangeland degradation, megafauna extinctions, and land grabbing. Each case constitutes an example of how drivers of change manifest themselves in Anthropocene problems, as well as the limitations or possibilities of deep-time, interdisciplinary perspectives to solve them. The review is not a comprehensive chronological account, but rather a synthesis of perspectives from diverse academic fields on key debates and representative topics. Experts on a given topic covered here might consider our treatment of that topic as lacking the necessary depth; our contribution is to draw connections across scientific domains in an effort to develop a conceptual vocabulary for talking about how African environments are produced through articulations of long-term social and ecological processes. Before turning to those drivers, we provide a general theoretical framework. Because of the long history of racially inflected perceptions of Africa, we begin with a critical reflection on discourse regarding the African past.

2. THEORETICAL FRAMEWORK

[The Anthropocene] requires us to both zoom into the details of intrahuman injustice—otherwise we do not see the suffering of many humans—and to zoom out of that history, or else we do not see the suffering of other species and, in a manner of speaking, of the planet. (7, p. 111)

Talking about Africa and its past has never come easy (1). Historiography prior to the 1960s independence era characterized African history as empty and static (8–10), or as stages in a progressivist narrative of societal transition from "traditional" to "modern" in which Africa always lagged behind other continents (11, 12; see 13). Where the natural world was concerned, the specter of racism always loomed, with African people figured as subhuman, somehow closer to nature than Europeans (8, 9). Consider the representation of so-called San people, often seen as archives of prior stages in human civilizational development rather than contemporary figures (14).

Far from empty and static, the history of African environments—their climates, flora, and fauna—has been marked by oscillation, flux, and contingency. The response of African people to these conditions has been marked by adaptation, flexibility, and innovation. Shaped by high-latitude glaciation cycles, Pleistocene-Holocene climates in Africa swung abruptly between humid-warm and arid-cool phases (15) that triggered changes in the patterning and selection of flora and fauna. Evidence suggests that the development of key behavioral and physiological adaptations in early hominins was linked to these swings and the heterogeneous environments they produced (16, 17), in concert with high levels of disturbance by fire and megaherbivores (18). For anatomically modern humans, archaeological findings describe a similar experience of flux and flexibility, including food production systems adapted to unpredictable rainfall regimes (19–21). The historical and anthropological records also identify these themes in Africans' responses to shifting and precarious sociopolitical and ecological conditions continent-wide (2, 3, 5, 22). Flux and adaptation will likely continue as central tropes in the future. Between the dramatic impacts likely brought about by climate change, human-induced environmental degradation, and population growth, African and global futures will be dynamic—and in need of innovative strategies.

Tracing these themes through social and natural systems from the Pleistocene to the Anthropocene furthers our understanding of the causes and implications of environmental change in Africa. First, knowledge of prior environmental conditions sheds light on the ways that current environmental patterns are shaped by biogeographical legacies (23, 24), with lessons for conservation regarding the response of biota to environmental change (25–27). Second, it can enable a post hoc testing of hypotheses that would be untestable today, such as using the Late Pleistocene as an analog for learning about the effects of continuing defaunation of large mammals on ecosystems

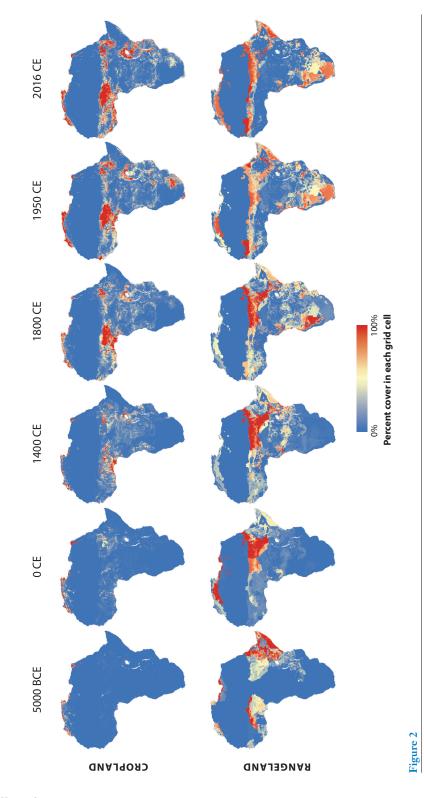
(28). Finally, knowing past human-environment dynamics can transform how we conceive of ourselves as humans. After all, living amid Earth's sixth mass extinction event, largely caused by human activities, raises philosophical and ethical questions (29–31) as much as it does questions about best conservation practices (32, 33). Even still, these potential insights are confronted by unprecedented Anthropocene conditions and describing these limitations is a goal of this review.

Learning these lessons requires simultaneous attention to ecological processes, historical contingency, and power. The onset of the Anthropocene has made scientists and policymakers broadly aware of the need to integrate the natural sciences, social sciences, and humanities. Envisioning humans as shapers of and elements within ecosystem processes is not new, but it has resurfaced with new models of human-environment interchange, including those based in socioecological systems (34), human niche construction (35, 36), the dialogic process that Donna Haraway calls "becoming-with" (37), and the metabolic rift (38). Natural scientists have grown anxious over the fact that even the most sophisticated understanding of ecological dynamics can fail to yield appropriate policy in the face of human politics and culture (39)—that solutions to environmental problems require political, not simply technical, sensibilities (40, 41)—and that sociocultural processes might represent unaccounted-for drivers of ecological change (33, 42). For their part, social scientists and humanists, traditionally focused on narrow spatial and temporal scales (for exceptions, see 43–45) and on strictly human affairs, have embarked on a radical rethinking of human life as a multispecies endeavor, reorganizing the boundaries of humanistic inquiry (37, 46).

Interdisciplinary scholarship is complicated by the political and intellectual commitments of humanists and scientists, however. Whereas natural scientists have sought to develop universal theories of human and nonhuman life, humanists have long sought to expose human difference and structural inequality. For postcolonial historians, for example, the Anthropocene calls forward a universal human subject that contradicts a long-held interest in accounting for the particularity and historicity of human experience (29). *Anthropos* itself is an Enlightenment concept that putatively describes a collective humanity but which can be used in practice to advance white, male, Christian ideals 31, 47, 48).

In this review, we hold on to this tension, arguing that the global nature of environmental change in the Anthropocene must also be understood in reference to its more localized histories and manifestations. We work across the concepts of ecosystem and environment. Ecosystems are open-ended networks of organisms in dynamic, abiotic contexts. Unlike the broader concept of environment, which does not imply relations between the elements that compose it, ecosystems are defined by those relations and exhibit system properties, such as resilience and critical transitions (49). High levels of disturbance or species turnover can trigger system shifts when impacts can no longer be assimilated (31, 49), an increasingly common possibility about which we know too little (33). Ecosystems are therefore local and historically specific, even if shaped by large-scale and system processes. Pleistocene climates, for example, have shaped the distribution of flora and fauna (23, 24), meaning that human or climate impacts today cannot be understood merely from contemporary conditions and ecological laws. Legacies of slavery, colonialism, capitalism, and postcolonial despotism also structure current ecological and sociopolitical formations, requiring attention to their specific effects and timing.

Although hominins have driven environmental change in Africa since the Plio-Pleistocene (50), their impacts have intensified dramatically with the population spread and growth of *Homo sapiens*; the rise of agriculture, states, and colonialism; and the advent of extractive, polluting, or otherwise destructive industries. This underscores the importance of recognizing human difference when assessing the role of "humans" in environmental change. Furthermore, like the tensions described above between the global and the local, the universal and the particular, we acknowledge the utility



Extent and intensity of land use in Africa for cropland and rangeland, 5000 BCE-present. Data from Klein Goldewijk et al. (51), used with permission.

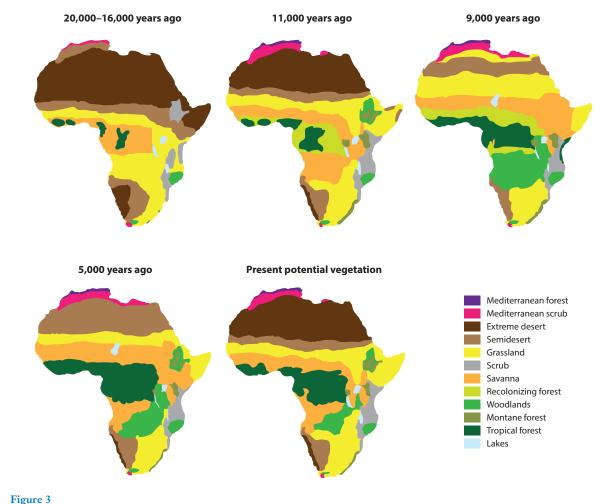
and pitfalls of defining the "African story" as the "human story" (11). Being the site of human origins, African history is human history, and yet also resolutely African.

Our chosen drivers represent the four most important as described in the interdisciplinary literature that span the sciences and humanities, and which demonstrate the dialogic process by which organisms shape and are shaped by their environment. Of the four drivers reviewed, climate operates as the broadest spatiotemporal scale, becoming pronounced in its effects during periods of varying temperature and rainfall (see Figure 1). The effects of agriculture and pastoralism are much patchier and shallower in time, dating roughly from the early to mid-Holocene with increasing intensity and spatial dispersion over time, particularly in the past century (see Figure 2). Broad-scale impacts of wild megafauna declined when they diminished in diversity and population size during the late-Quaternary extinctions 80-7 kya, and further with widespread hunting and habitat destruction during the past 150 years, while sometimes locally intensifying as they become concentrated in designated conservation areas (see Section 5). Potential environmental change brought about by ICC does not appear until the late first millennium of the Common Era with Arab trade in goods and slaves across the Sahara and via the Indian Ocean, and, later, European trade and plantation agriculture. However, early African states predated these foreign interventions by several centuries and also had imperial tendencies (12) that may have manifested in environmental change, although understanding of these effects is limited. Such changes must mostly have been localized up to the contemporary moment, but have broadened with growth in human population, natural resource extraction industries such as timber and oil, and agriculture.

3. CLIMATE

In this section, we describe the nature of African climates and their effects on ecosystems before zooming in on one site where these effects have been particularly dramatic in the recent past, the Sahara-Sahel zone. The Pleistocene and Holocene climates of Africa featured repeated oscillations in temperature and rainfall, shifting between humid-warm phases (pluvials) and arid-cool phases (interpluvials), which were in many cases linked to climate fluctuations in the Northern Hemisphere and Antarctica (52, 53). Across the Pliocene-Pleistocene transition, African climates varied at increasingly longer intervals, from 21 to 41 thousand years (15). The oscillations also increased in amplitude and length during a steplike transition period in the Late Pliocene to Middle Pleistocene at 2.8 Mya, 1.7 Mya, and 1.0 Mya (15). There were 11 Pleistocene glacials in total, with the Last Glacial Maximum at ~21 kya (52). During the Holocene, smaller climatic oscillations between humid-warm and arid-cool conditions continued, although these were generally more severe in amplitude at lower rather than at higher latitudes (52). During the latter half of the Holocene, changes have been minimal, the strongest of which have been north of 15°N with diminished monsoons and substantial drying (54).

These climate changes have had important effects on flora and fauna. During the Middle and Late Pleistocene, Africa's biomes expanded and contracted repeatedly in response to the glacial-interglacial climate oscillations (see **Figure 3**). During humid-warm phases across the Pleistocene and Holocene, forests expanded into the semideserts in the Northern Sahara, the savannas in equatorial Africa, and the mountain scrublands south of the Sahara; during arid-cool periods, the Sahara expanded into semidesert areas, while savannas and grasslands with arid-adapted species expanded into lowland forests (55). These fluctuations would have had important effects on large-mammal population size and structure—directly, from drought-related mortality, and indirectly, through the vegetation changes that fluctuations brought about. For example, the period between 2.8 and 1.8 Mya was a period of accelerated turnover in Eastern African fauna at least partly driven by climate change (56, 57). Across Western, Eastern and Southern Africa, the pluvial-interpluvial



Vegetation change in Africa, 20 kya–present. Adapted from Adams & Faure (61).

pattern initiated vicariance events in populations of ungulates when their savanna habitat was fragmented by forest expansions (58). With a series of megadroughts beginning in the Middle Pleistocene, fluctuation has been particularly abrupt and severe in Eastern Africa, even if the overall trend has been toward increased humidity (59). These droughts are thanks to the existence of so-called amplifier lakes, brought about by the development of the Cenozoic East African Rift System during the Early Miocene (60).

African ecosystems are rainfall- and disturbance-limited, but atmospheric CO₂ may have more important effects than often recognized.¹ Increased atmospheric CO₂ levels can promote C₃ vegetation over the C₄ grasses by diminishing the usefulness of the C₄ photosynthetic efficiency (63). Recent research indicates that increases of atmospheric CO₂ are triggering changes in plant composition with cascading effects for biodiversity and ecosystem function (63–65). Although abrupt regime shifts are probably unlikely except at local scales (66), there is precedent for predictions

¹More work is also needed to assess the importance of temperature fluctuations (see 62).

that the increased atmospheric CO₂ projected by the Intergovernmental Panel on Climate Change (IPCC) (67) will have large-scale effects on ecosystem structure and function over the long term. This happened, for example, with the expansion of C₄ plants in sub-Saharan Africa in the Late Miocene (68) and their contraction during the terminal Pleistocene, when atmospheric CO₂ concentrations were low (26). Zooarchaeological evidence in the South African Cape Region suggests that the expansion of woody vegetation into grasslands could have led to declines in ungulate grazer populations (26). Although the expansion of woody plants could also have been prompted or accelerated by the herbivore declines, the findings point to an important area of research into the role of atmospheric CO₂ in prompting cascading environmental changes.

Human ancestors were particularly affected by these climate fluctuations and their attendant ecosystem effects. The climatic pulses from 5–1.8 Mya triggered periods of speciation and extinction in the hominin line, during which key evolutionary adaptations were selected, including habitual bipedality, stone-tool use, long-endurance mobility, rapid brain enlargement, and symbolic expression (15–17). There is debate as to the mechanics of the process, but indications are that climatic pulses rewarded behavioral versatility in adapting to a wide diversity of habitats (16). Fluctuations also shaped the distribution and spread of early humans. Hominin populations dispersed and expanded during wetter periods when resources for migration were in relative abundance (16, 60, 69). In effect, early human survival in Africa entailed a negotiation of contingent change and environmental variability—not a mastery of the environment—and has been inscribed into human behavior and morphology over evolutionary time (16).

3.1. Sahara-Sahel Dynamics

The dynamics of the Sahara-Sahel transition represent an important example of how climate oscillations have shaped African environments, of how humans have adapted to climate shifts, and of the value of deep-time histories for assessing shallow-time changes. Although the Sahara zone today is nearly uninhabitable, during the Middle and Late Pleistocene it was an expansive grassland ecosystem (see **Figure 3**). Research points to the former existence of large watercourses running north–south across the Sahara during the last interglacial (70). The area aridified until ~15 kya with the onset of the African Humid Period, when a northward shift in the monsoon belt initiated a northward movement of the Sahel biome (commonly delimited by the 200-mm rainfall isohyet) and tropical grasslands, and a southward expansion of Mediterranean scrub and woodlands (61, 71). These vegetation zones receded once again, however, between 8 and 4.5 kya, when an abrupt desertification was triggered by a combination of orbital forcing and positive feedbacks between high-albedo desert sands and atmospheric circulation (49), the latter of which may have been instigated by widespread human adoption of agriculture and pastoralism in Northern Africa (71; see also Section 3.2).

The Holocene cycles of humidity and aridity had strong effects on human settlement in the region, as humans tracked these climate changes for hunting, pastoralism, or farming (72, 73). They had political consequences, too. When trade networks opened or closed, states and ruling classes on both the Western and Eastern edges of the Sahara exploited new opportunities to control people and goods (73, 74). Despite the general shift toward more arid conditions from the mid-Holocene, Sahelian and Sudanic Africa experienced wetter conditions between the sixteenth to mid-eighteenth centuries, a period that coincided with the European and Arabic colonial expansions into Africa and the "Little Ice Age" to the north (54). This was followed again by a much drier and drought-prone period of the nineteenth and twentieth centuries (75), during which time African territories were divided among European states and colonial powers accelerated their efforts to extract natural resources, including plantation crops and minerals.

Severe Sahelian droughts in the postindependence period prompted widespread famines among people living in the region. Concerns emerged about the southward expansion of the Sahara in the early 1970s and mid-1980s and of the potential role of humans in the process, with some suggesting that droughts were amplified by feedback mechanisms when human removal of vegetative cover increased surface albedo (see 49, 75). Although some believed earlier in the century that desertification was occurring there (76), the process became an object of broader concern after the 1977 United Nations Conference on Desertification in response to the Sahelian famines. The term desertification is often used ambiguously, and alarm over its spatial extent has been exaggerated in some cases (75, 76), but it is increasingly believed that land surface conditions affect convection and can thereby act as a trigger for localized rainfall anomalies (75). Additionally, the removal of natural vegetation occurring in the Sahel likely does have enduring effects, given the strong ecological filtering of plants attempting to establish themselves in stressful environments. However, anthropogenic land surface changes are one among many such triggers or drivers, including sea-surface temperatures and features in the upper atmosphere. At smaller scales, it remains possible that the practices of farmers represent responses to climate change rather than causes of it (77). Rainfall has recovered since the driest periods during the 1970s and 1980s, although there have been changes in the peak and the spatial distribution of rainfall (75). The "regreening" of the Sahel since the 1980s, documented through time-series of remotely sensed satellite data (i.e., Normalized Differential Vegetation Index values), has reflected these changes in rainfall, but nonlinearly (78). Vegetation response has varied geographically and in some places shifted toward a less forested condition rather than returning to predrought conditions, indicating the complexity of climate-vegetation relationships in that region and the difficulty of parsing anthropogenic influences across a broad spatial scale (78).

3.2. Anthropocene Challenges

Sahara-Sahel dynamics demonstrate not only the importance of human adaptive response to climate fluctuation, but also the tremendous challenges ahead. Over the past 50–100 years, Africa has seen a warming trend that will continue across the continent, with medium scenarios suggesting an increased 2–6°C mean annual temperature increase by the end of the twenty-first century. The overall trend is toward greater aridity and greater interannual variation in rainfall, but with localized rainfall increases. Northern Africa and the southwestern regions of Southern Africa are likely to see a decrease (67). Eastern and Western Africa could see an increase in rainfall overall, but this will include increases in the frequency of extremely dry and wet years (67). These trends are expected to have serious consequences for crop production. Yields of cereals, especially maize, are expected to be negative across the continent, and drought will continue to be the natural hazard most affecting African crop and livestock production (79). The survival of flora and fauna will be challenged, particularly in relation to habitat changes. African palms, for example, an important resource for humans and nonhuman animals, will likely see substantial decreases in suitable habitat as humans transform landscapes and climate changes render current distribution areas less suitable for them (80).

4. AGRICULTURE AND PASTORALISM

The unpredictable, dynamic, and heterogeneous environments described in the previous section have structured the peopling of the continent (81), the use of domestic plants and animals (20), and social and political formations (72), all with implications for environmental change. In this section, we review literature on the environmental impacts of smallholder production (for

large-scale production, see Section 6), with an in-depth focus on rangeland degradation. These impacts date roughly from the early to mid-Holocene when those two forms of food production began to intensify and spread across the continent. We show that peasant agriculture and pastoralism are often assigned blame for not being modern and sustainable, but a deeper look reveals often environmentally appropriate, flexible forms of food production. Nevertheless, these strategies are increasingly put under stress by population growth and land alienation.

As shown in **Figure 2**, effects of agriculture and pastoralism have been localized and geographically dispersed, but are expanding. Domestic cattle originating from Southwest Asia appear in the archaeological record ~8 kya in the Nile Valley, and then westward and southward over subsequent millennia (71, 82). Domestic sheep and goats appear around 7 kya, introduced from Southwest Asia, the Middle East, and Southern Europe (19, 21). They moved southward into Western and Eastern Africa with the Sahara desiccation at around 4 kya, inhabiting Eastern Africa broadly by 3 kya (82). Around 5 kya, Bantu agropastoralists began migrating outward from the western areas of contemporary Cameroon, reaching South Africa on an eastern route by 3.5 kya and, on an eastern route, reaching Mozambique by 1.8 kya, although the specific timing and direction of spread are contested (83).

Africa is considered a "frontier continent" (81), colonized by groups splintering off of existing polities through expulsion or discontent, who then adapted to often inhospitable climates and disease geographies. Frontier groups were often reabsorbed by their original polity as it expanded into frontier territory (72)—although probably not in the earliest waves of migration (83)—allowing for the conservation and spread of cultural traits (81). The pace and direction of their movements were structured by the environments they encountered (84), but made possible partly because of Africa's low population densities. Unlike in Europe from the fifteenth century onward, where land was limited compared to available labor, the reverse has been true in Africa (72, 81, 85).² Because labor—not land—was the primary limit to agricultural production in Africa especially in the precolonial period, political leaders needed to invest in social relations (87) or "wealth in people" rather than seek wealth in resources (88).

Abundant land and heterogeneous, unpredictable environments had broad ramifications for human-environment relations, including plant and animal domestication. Although much has been made of the fact that domestication occurred comparatively late in Africa, with some observers taking it as evidence of African backwardness (see 20), the contexts and motivations in Africa were unique. Domestication developed in a fashion opposite to other parts of the world: Domestic animals appeared thousands of years before domestic plants and were produced by small groups of mobile cattle herders (19). Contradicting the view that settled agriculture represents a linear, inevitable step in human advancement, archaeological evidence shows some African groups abandoning agriculture for pastoralism; shows others adopting a mosaic of hunting, gathering, agriculture, and pastoralism; shows agriculturalist and pastoralist groups coexisting in complementary relations of production; and shows pastoralism emerging as a response to efforts at control by centralized agricultural societies (19-21). Biological and ecological barriers to domestication may have been important, as well. For instance, high outcrossing of plant domesticates, including African grains such as sorghum and pearl millet, can prevent the genetic isolation necessary for phenotypic modification (19, 20), meaning that people in the Sahel were manipulating and possibly cultivating multiple grains over the course of 5,000 years, but with little phenotypic change (89). The impacts of human food production intensified with the incorporation of Iron

²However, Manning (86) has proposed an upward revision to population estimates from 1450–1950 based on as-yet-unpublished data, which could complicate this long-standing point.

Age agriculture. Humans became able to clear larger areas for production (44), and significant deforestation likely resulted from the fuelwood demands of iron production as early as 300 CE in East Africa (90, 91). Archaeological evidence of large-scale precolonial land transformation is limited, however.

These food production systems have been flexible and opportunistic in response to a patchy geography of disease and food availability, where increasing predictability was the goal rather than increasing yield (19). In closed habitats and bushy savanna regions of Africa, for example, where the tsetse fly exists and transmits the virus that causes trypanosomiasis, domestic cattle suffer often fatal infections that severely limit pastoralism in those areas (21). The tsetse zone has shifted latitudinally by several hundred kilometers in Sahelian and Sudanic Africa during pluvial-interpluvial phase shifts, as well as with the expansion and contraction of forests elsewhere. These diseases curtailed territorial expansion or migration of pastoralists, meaning that pastoralism developed in dialogue with the disease environments they encountered, an inverse relationship to tsetse biogeography (21). But domestic animals were critical players in the expansion of African populations into new territories and continue to play an important role today. African goat breeds show considerable adaptation to local conditions, such as size and heat tolerance, and were probably used to "domesticate" the landscape in tsetse zones, clearing areas of bush before cattle were introduced (21). The pace of southward colonization by pastoralist people was slow and it was only in the first millennium BCE that sheep are confirmed to have reached Southern Africa, 500 years before agriculturalists (21). Thus, it took some 8,000 years for pastoralism to reach the Cape from its first appearance in North Africa, a testament to the numerous ecological and epidemiological barriers to diffusion (21; see also **Figure 2**).

Adaptive approaches to food production stretch from the mid-Holocene, when African people took up imported domestic livestock and diversified agricultural systems gradually spread across the continent, through to the Anthropocene, when farmers have adjusted their crop and livestock production to the vagaries of many African climates (e.g., 92). Whereas Western models tend to emphasize maximizing efficiency, such a strategy is not sensible for farmers in many arid and semiarid regions, for whom maximizing flexibility, diversity, and adaptability to shifting environmental conditions is critical (19, 22), such as diversifying crops to increase returns from croplands with variable soil properties (93). A failure to recognize the importance of flexibility has hampered the implementation of development programs seeking to boost smallholder production (22, 93).

4.1. Rangeland Degradation

Rangelands include grasslands, savannas, scrublands, and wetlands that support livestock production and cover 25–45% of Earth's surface, depending on how they are defined, with approximately 30% of that area located in Africa (94, 95). Rangelands are often subject to variable climate (95) and vary in their inherent propensity for degradation (94), raising challenges for those who seek to discern the relative importance of climate variables and human use to driving rangeland degradation or change. Rangeland degradation refers to a decline over time in the diversity and productivity of rangeland vegetation, sometimes manifesting in increases in the proportion of woody to herbaceous species, the proportion of unpalatable to palatable species, or soil erosion and compaction (94, 95). Concerns about rangeland degradation flared in the colonial era, particularly in the early twentieth century. These concerns grew more pronounced with time, and in the 1980s it was estimated that 85% of rangelands were facing degradation (94). However, the fact that alarm has been high for nearly a century without evidence of ecological collapse leads some to question the viability of degradation measurements (94). This does not mean that degradation has not taken place, but rather that contemporary signs of degradation might result from human disturbance

during an earlier period or from biophysical conditions that predispose some areas to degradation more than others (94).

The alienation of land by states and the conversion of rangeland to agriculture, which gathered pace in the twentieth century, increased land pressures and drove land degradation at the same time that human population increased (96–98). In response, colonial states and conservation scientists made efforts to address the issue. In particular, soil erosion, deforestation, and desiccation emerged as urgent problems. However, the ecological impacts of African pastoralism were called into question by research in the 1980s and 1990s, which showed that charges of "overgrazing" in African pastures have tended mistakenly to presume an equilibrium model of ecological succession, in which disturbance pushes a system linearly away from a climax state (see 99). In such a case, pastures have a definable "carrying capacity," which, when exceeded, leads to a degraded state. However, nonequilibrium dynamics (100, 101) prevail in many African systems with high coefficients of variability in rainfall (99). Under such conditions, abiotic factors such as climate are more determinant of range condition than biotic ones such as livestock density, and a variety of alternate stable states are a more likely possibility than linear succession to climax. Furthermore, Homewood & Rodgers (102) showed that a carrying capacity can only relate to a specific management goal. For example, Eastern African pastoralists take a higher stocking rate than a capitalintensive rancher would, obtaining low rates of production per animal, but high overall output per unit of area. Actual stocking levels can exceed estimated carrying capacities for decades at a time (101). Cumulatively, this research brought a paradigm shift. Whereas blame for degradation had been assigned to African smallholders as ignorant or irresponsible stewards of their land, livestock densities were newly understood to represent sensible strategies in the face of strong environmental variability (22, 101, 103, 104; see also 99). Current consensus is that rangeland systems are not either equilibrial or nonequilibrial, but rather they can be characterized by dynamics from both and at different spatial or temporal scales (105, 106). This conclusion does not rule out the possibility of livestock-induced land degradation. However, it does suggest it might be difficult to diagnose and that nuanced models of land management—fit to African environments—are needed.

4.2. Anthropocene Challenges

These distinctive processes of domestication, frontier-making, and food production suggest that imported models of civilizational progress do not explain African cases well (11, 12). It remains to be seen if these adaptive strategies will be sufficient to endure the impending climate changes described above, or the demographic changes predicted—with the current human population of 1.2 billion in Africa rising to 2.5 billion by 2050 and 4.4 billion by century's end (107). Some authors (e.g., 93) argue that population growth is not inherently detrimental to environments and could actually improve sustainability of communities through the intensification of indigenous, flexible systems of production that have suffered from low labor supply. Population growth and consequent land use also could offset some natural processes, such as the anticipated expansion of woody plants due to increased atmospheric CO₂ (108). However, as described in Section 6, the enclosure of territories that began with colonialism, the conversion of pastureland to agriculture, and population growth have all conspired to diminish people's ability to move with and adapt to change.

5. MEGAFAUNA

Large, terrestrial mammals known as megafauna are powerful drivers of environmental change, but their effects have diminished with the decline of their diversity, population sizes, and geographic dispersion. In this section, we describe what is known about megafaunal ecosystem effects and how they articulate with climate changes or human activities, before turning to focus on the causes and consequences of megafaunal extinctions. Using a trophic carnivore-herbivore cascade definition (28), megaherbivores (≥1,000 kg) and large herbivores (45–999 kg) are distinguished from megacarnivores (≥100 kg) and large carnivores (21.5–99 kg). In contrast to the contingent and subtle effects of African people's food production systems described in the previous section, here we show that human impacts on megafauna have been dramatic.

Being without predators, megaherbivore and megacarnivore populations are bottom-up regulated by available food resources, in contrast to animals with predators, which are top-down regulated through predation. In consequence, the loss of megafauna can potentially allow population increases of trophically lower organisms, modulating their ecosystem effects, as has been found with the Yellowstone reintroduction of wolf populations (109). Megaherbivores and large herbivores can assist in seed dispersal, particularly of large-seeded plants; create landscape heterogeneity in woody-herbaceous patterning through trampling and consumption of woody species, promoting functional and species diversity in plants and other organisms; act as a source of food for predators and scavengers; shape the intensity, frequency, and spatial distribution of fire; and accelerate nutrient cycling by consuming large amounts of plant biomass (28, 110-114). In addition to regulating large mammal populations through predation, megacarnivores create a patchy landscape of fear for herbivores, shaping the ecological filtering of vegetation (115). Megaherbivores such as elephants (Loxodonta africana), for example, increase the heterogeneity of browse in savannas vertically, creating a multilayer canopy pattern when their trampling induces plant response by trees, the resprouting of which can also improve forage quality by increasing carbonnitrogen ratios (116). Elephant-damaged trees have also been found to serve as associational refuges, increasing understory biomass and species richness by indirectly protecting them from grazers (113).

Megafaunal impacts on ecosystem structure and function are also modulated by climate, fire regimes, human disturbance, and other factors. The formation and persistence of savanna ecosystems constitute an important example. Savannas are unstable states that can transition between grassland and closed forest (117), featuring competition and facilitation between woody and herbaceous plants, niche separation, and disturbance by fire and herbivory (63; see also 24). At large spatial scales, abiotic and biogeographical legacies are understood to be determinant of savanna structure, whereas community dynamics and a mosaic of disturbances are determinant at smaller scales (24). Fire acts as a source of consumer control with implications for evolutionary adaptations, plant ontogeny, and the filtering of plants by functional traits adapted to prevailing fire regimes—particularly in mesic savannas, where fires are most common (63). Grazers promote woody vegetation by removing the herbaceous competitors, exerting a negative effect on fires that are fueled by herbs, whereas browsing has the opposite effect, promoting herbaceous plants and therefore fire, as well as increasing the likelihood of woody fatality during fire—feedbacks between these elements can lead to discontinuous shifts in vegetation (117). The effects of fire in limiting woody plant growth could diminish somewhat under increased atmospheric CO2 levels with current climate change, promoting faster growth for plant species such as trees that use the C₃ photosynthetic pathway over C₄-pathway grasses and enabling them to reach a large enough size to persist through fires (118). But browser release has also been shown to override these feedbacks irrespective of grazer pressure and to promote dramatic increases in woody cover (119) that can persist even after browser reintroduction (120). As shown in the following subsection, understanding the ecosystem effects of megafauna removal represents an urgent research priority for environmental scientists in the Anthropocene.

5.1. Defaunation

Appreciation for the ecological function of megafauna has increased in light of their endangerment, extirpation, and extinction. Large, terrestrial herbivores and carnivores declined dramatically during the Late Pleistocene and early Holocene, before which time they occupied most of the world's habitats (28). Declines continue today (121−123). Approximately 90 genera of mammals weighing ≥44 kg were lost globally since the Late Pleistocene (124). Africa lost fewer species than other continents, but the losses were nevertheless substantial. Currently, 140 species of mammals weighing ≥10 kg exist in Africa, down from 158 in the Late Pleistocene; of the 88 species weighing ≥45 kg from that time, 72 are extant (based on data from 114 and 125). The population sizes and species richness of large mammals in Africa are higher than in other regions of the world (28, 111), but they continue to decline due to hunting, habitat loss, and habitat fragmentation (121, 123, 126, 127).

The climate oscillations of the Pleistocene had substantial effects on the population dynamics and ranges of ungulates as seen in their phylogeography, with divergence events occurring during the pluvial phases that brought forest expansion into previously continuous savannas and created expansive refugia in Western and Southern Africa as well as a mosaic of smaller refugia in Eastern Africa (58; see also 128). Although megafauna and mesofauna distributions have responded to past climate changes, humans are likely to have been the primary driver of prehistoric megafauna extinctions, when evidence of the timing of losses is squared with evidence regarding changes in climate, vegetation, and human behavioral adaptations. Abnormal rates of megafaunal loss first appear in Africa among proboscideans and carnivores such as saber-toothed cats during the period 2.8–1.8 Mya, which saw increased turnover in Eastern African fauna, paralleling climatic change (56). However, this period also includes the earliest evidence for persistent carnivory among hominins at \sim 2 Mya (57). Werdelin & Lewis (50) show that carnivorans only saw minimal turnover until the latter part of that period, leading them to suggest that the guild's loss of functional richness and evenness is likely explained by the evolution of hominins into carnivore niche space.

Most debated are the causes of the late-Quaternary Extinctions (LQE), the global loss of large, terrestrial mammal taxa 80-7 kya, although direct and indirect human influence is likely, perhaps in combination with other environmental factors (124). Twenty-four large mammal species became extinct in Africa during the LQE, most of which were grazers (129). This has led to the suggestion that habitat change was likely the primary driver of their extinction (129, 130). It is true that isolating human impacts on megafauna populations from climate and other factors will not explain the dynamics of species losses entirely, as mid-Holocene regional extirpations of large-bodied herbivores may be triggered or amplified by climate processes (e.g., 131). However, habitat-centered explanations do not consider the wide availability of grasslands across the continent through this period and that most megafauna have wide distributions; as such, continental-scale extinctions cannot be explained by local or regional vegetation dynamics. An alternative explanation could be that open-habitat species were easier to locate and less dangerous to hunt, e.g., in terms of exposure to carnivore attacks. Heller et al.'s (132; also 124) findings suggest that the LOE in Africa could have been as severe as other continents, where many more species were lost, if Africa had not featured more refugia for large mammals in areas hostile to human habitation, such as tsetse zones. A contributing factor to the lower LQE in Africa may also be that Africa already lost many sensitive taxa in response to earlier hominids (see above), and simultaneously was

³However, forest expansion would have promoted forest-dwelling fauna, such as primates and forest elephants (L. cyclotis).

experiencing a climate-linked diversification of bovids (128) with high reproductive rates and likely high tolerances of human hunting.

Ecosystem changes likely resulted from megafaunal extinctions, with cascading consequences in floral and faunal communities (111, 133–136). For example, Central Africa features relatively low alpha diversity in tree species compared to other wet tropical regions in South America and South Eastern Asia, contradicting a fundamental generalization of biogeography: that ecosystems with similar environmental conditions share broad similarities. There is now considerable evidence that this was driven by the legacy effects of aridity, megadroughts, and fire regimes that caused evergreen forests to contract during the Pleistocene and Holocene, or earlier (137, 138). However, Terborgh et al. (139, 140) suggest that the existence of populations of megafauna such as elephant (*L*), gorilla (*Gorilla gorilla*), and forest buffalo (*Syncerus caffer nanus*) could represent a supplementary factor. They show differences in hectare-scale diversity of small and large trees between African and South American rainforests, with anomalously low diversity in the small tree class in Africa. They attribute these differences to megafaunal influence, whereby megafaunal trampling and consumption lower the density of small trees, with this effect much reduced in South America since the severe LQE (see also 114). More research on ecosystem effects of the LQE is needed to help explain current vegetation patterns and inform conservation strategy (25–27).

5.2. Anthropocene Challenges

Megafauna in general capture the problems of multispecies coexistence in the Anthropocene: Even with recognition of their ecological value, desires to conserve populations can conflict with available conservation land (141). The conservation statuses of many African megafauna are on a declining trajectory today (110, 111), with rapid population declines in both megacarnivores (127, 142) and megaherbivores (143, 144). The threats include not only hunting (121, 122), but also fencing and habitat destruction or fragmentation stemming from human activity (126, 127, 145). Thus, for example, the declines of large herbivores in savanna systems may reduce beta diversity and the spatial heterogeneity of woody vegetation (112), particularly as fencing and artificial water points alter the way that large herbivores move through a landscape (146). During the Pleistocene and Holocene epochs, available land may have enabled the recovery of ungulate populations that could flee drought-stricken areas, but today this movement is impeded (146). Whether the kind of habitat patchiness that will prevail in the Anthropocene presents opportunities for cospecies life, as suggested by human food production described in Section 4, or merely dangerously isolated populations and concentrated resources remains to be seen.

6. IMPERIALISM, COLONIALISM, AND CAPITALISM

The final set of drivers of environmental change we review has a patchy spatiality, most pronounced near centers of power, and a comparatively shallow temporal frame. It also represents a wide variety of land transformation types, which we describe in this section, including the fragmentation of geographic space, large-scale agriculture, and even conservation efforts. As scholars in social theory have recently shown (3, 5), Africa has been at the front lines of political economic changes despite its reputation as a place marked by timeless tradition. Neoliberal capitalism, for example, reached the continent at least a decade before the Global North (3, 5, 147). Innovation comes from both "sides": On one hand, it comes from states and colonial and capitalist enterprises that saw Africa as a site of experimentation in economic restructuring (147), agronomy, and conservation (148; see also 149). On the other hand, it comes from everyday people before, during, and after colonialism who navigated unpredictable natural and political environments (2, 4).

With the rise of states and long-distance trade networks in the late first millennium CE (12, 43), the Middle Eastern and then European conquest of large territories in Africa, and more contemporary forms of capitalist extraction, African environments became subject to new, more intense forms of transformation (see **Figure 2**). This process accelerated in the nineteenth and twentieth centuries, which witnessed the intensification of crop production through plantations and slavery (85, 86, 150), the intensification of livestock production (96, 151), and the introduction of exotic species (152). These changes accompanied a rethinking of the meanings associated with environments (153), and this process of redefinition entailed what Carolyn Merchant (154) has called ecological revolutions, a transformation of the ways that environments are engaged by humans along lines of race, class, and gender—and a subsequent transformation of the environment itself.

One important site of transformation by ICC projects has been the alienation of land through enclosure and state boundaries, the effects of which diminish with distance from centers of state power. As noted earlier, the high ratio of land to labor had shaped African societies over centuries. The enclosure of land by colonists upended this arrangement, as land became finite and labor became abundant (72). Pastoralist livelihoods were particularly affected when they became targets of state administration. Like those who practice other nonsedentary livelihood strategies such as shifting cultivation, pastoralists frustrate governments interested in fixing populations territorially and institutionally (97, 155). War, urbanization, agricultural expansion, and environmental conservation during the past century have further circumscribed pastoral activity (95, 97, 98, 155, 156). Here it can be seen that not all effects of ICC on environments and environmental management are coherent and some are quite contradictory. For example, common property regimes have been variably undermined and promoted. Although common property systems are often thought of as obstacles to modern management, being administered by unelected chiefs, chiefs' authority was partly a product of colonial "indirect rule" (98, 157–160).

Plantation agriculture represents another important form of land transformation. Although it was established in Africa as early as the sixteenth century (86), the nineteenth century was a period of dramatic expansion in plantation agriculture. Arabs of Oman and, later, British colonists established spice, tea, and coffee plantations on the coasts of East Africa (85); the British and Portuguese established sugar and cotton plantations in Southern Africa (161); and British, Portuguese, and French colonists established plantations of rubber, palm oil, cocoa, and peanuts in Central and Western Africa (86, 162). Demonstrating that the story of African interaction with ICC processes is never simply one of either domination or resistance (163), Africans themselves have embraced introduced crops and proliferated them through innovative planting and selecting processes, including manioc, bananas, and maize. In doing so, African smallholders have ultimately privileged a small number of crops over the extant, heterogeneous flora occurring naturally. For example, white maize has become the most preferred cereal nearly everywhere that it can be grown (92). The bulk of production is in Southern Africa, where suitable conditions exist: Maize cultivation accounts for as much as 90% of cultivated land in Malawi (92), and more than 50% of total calories are derived from maize alone in Lesotho, Zambia, and Malawi, 43% in Zimbabwe, and 31% in South Africa (164).

Thus, the innovations of ordinary Africans are not necessarily benign. In Southern Africa, the cash economies created by mining employment indirectly increased agricultural production by smallholders who were newly able to purchase agricultural inputs such as ploughs and improved livestock—but also encouraged land degradation (148, 165), particularly when in combination

⁴These studies have primarily been concerned with the political, economic, and social implications of plantation agriculture, and more work is needed to assess the environmental legacies of these agricultural practices.

with increased land pressure due to population increases and land expropriation by settler colonists and national elites (41). Furthermore, efforts to transform African environments for industrial-scale food production and resource extraction were not an exclusively exogenous practice. In the period immediately following independence, several African states pushed to "modernize" their agricultural economies through large-scale enterprises. Postcolonial leaders such as Julius Nyerere in Tanzania saw the conquest and exploitation of nature through large-scale schemes as a next step in their struggle over imperial powers—they turned their fight to "not man but nature" (72, 166). Nyerere's *ujamaa* villagization scheme, inspired by the United States Tennessee Valley Authority, saw as many as 5 million people relocated into "improved" villages where monoculture row-cropping was promoted by state agronomist extension officers before collapsing (166).

Amid the environmental fallout from these intensified human impacts, however, ICC enterprises set the terms for ecological conservation (4, 151, 167), complicating Africans' ability to conserve on "African" terms. State conservation efforts done in the name of environmentalism often entailed (sometimes violent) expropriations of land and resources from marginal populations, giving the lie to the presumptions that the state is the natural arbiter of competing claims to natural resources, and that military protection of conservation areas is therefore a legitimate response (4). In some cases, conservation was more a means to maintain a social order than environmental protection per se. In South Africa, concerns about land degradation on "native reserves" were linked to fears that rural agricultural collapse might send destitute Africans to urban centers in large numbers and upset the segregationist order of Apartheid (168). Colonial solutions were sometimes ill-informed; driven by stereotypes or exogenous, inappropriate science; or even destructive (148, 169, 170). In the case of nature reserves, officials sought to purify human ecologies as nature spaces despite their having been shaped by centuries of human use and manipulation (4). Although rural people are sometimes blamed for degradation due to their use of common land tenure or other arrangements that rely on noncapitalist social practices, market-oriented production such as Tanzania's *ujamaa* program (171), wool production in South Africa (151), and beef production in Botswana (96) have been destructive precisely because they were linked to capitalist markets that encouraged production to outpace environmental limits. A broad-brush critique of colonial-era European scientists as ignorant and racist is not warranted, however, given that many went to great lengths to learn from local, African people and sought to appreciate the nuance of complex ecosystems that confronted them (149). Contradictorily, then, African insights into the environment have been internalized into European conservation even as African ways of knowing have been marginalized (4, 13). On the whole, too many of the solutions to African land degradation have derived from outside the continent (4, 169). Developing African solutions that might reconcile Western science and indigenous knowledge production is an important area of new research (167).

6.1. Land Grabbing

The conversion of land to plantation agriculture represents a tremendous potential source of future environmental change, given growing demands for food and biofuel production—and because it simplifies the plant community, destroys habitat for native flora and fauna, and increases land pressure for smallholders. Food production in Africa was self-sufficient until the 1970s, but then the continent started to experience a decline in per capita food production, one reason that African countries grew increasingly dependent on food imports and aid, alongside the expansion of the humanitarian aid industry (172). Large-scale row-planted monocropping does occur today, but smallholder production remains predominant. However, the past decade has seen increasing concern over so-called land grabbing (173). Referring broadly to large-scale (trans)national

commercial land transactions, land grabbing is a global phenomenon anchored in Sub-Saharan Africa. Indications are that the phenomenon has been rapid and widespread, but the precise numbers are disputed (174, 175). What is clear is that, although these projects are often undertaken with the ostensible goal of addressing a "global food shortage," most are undertaken for energy production in the form of biofuels and disadvantage everyday people (173). Some of the continent's most productive and well-watered lands are sought, suggesting possible implications for biodiversity and conflict (176). That most of the land being "grabbed" is governed by customary tenure and not private title points to the important fact that land grabbing is often executed by national elites (160, 173, 174). The specter of large-scale, monocrop plantation agriculture in Africa rightfully raises concerns for African ecosystems, as historical cases of such conversions have had serious negative social and environmental consequences (162, 166, 171). However, there is limited evidence as yet of large-scale land conversion (173), suggesting that the speculative purchasing of African land might currently be impacting African environments less than African livelihoods, as tracts of land are legally removed from common property regimes and put in play as assets for speculative trading until eventually put under the plough.

6.2. Anthropocene Challenges

What land grabbing does show is an example of how historical arrangements can have legacy effects—what Ann Laura Stoler (177) calls imperial debris—not unlike the legacy effects of Pleistocene climates on the contemporary distribution of flora and fauna (24). Wily (178; see also 173) points out that many postcolonial governments inherited land rights legislation from the colonial era. Such legislation did not promote smallholder rights, but rather the centralization of control by the state and the opening up of resources to outside investors—it is precisely these legalinstitutional structures that have enabled the large-scale sale of land today (173, 178, 179). The situation recalls other cases of legacy effects. Extant trade networks, for example, have been mobilized to advance new goals, such as when colonial institutions were repurposed for humanitarian aid industries (73) or when, in the early nineteenth century, slave-trade networks shifted to ivory (44). A similar situation prevailed when, upon the end of slave trade in Ghana, slave owners became employers and the growth of export agriculture replaced slave-based commercial farming (180). In sum, these cases draw attention to the ways that environmental impacts of human activities are historically situated and textured by existing class structures, even if they are also reimagined for new circumstances. As with our other focal drivers, ICC processes appear set to intensify in the future under conditions of climate change and human population growth, as efforts by states and multinational corporations to secure land and natural resources expand into new territories.

7. SYNTHESIS AND CONCLUSION

African environments from the Pleistocene to the Anthropocene have been marked by oscillation, contingency, and flux, requiring flexible, adaptive strategies for human survival. This history holds lessons for thinking about the causes, implications, and possible responses to future environmental change. Climate shifts between arid-cool and humid-warm phases led to latitudinal shifts in vegetation zones and repeated expansion and contraction of open and closed vegetation. The hominin line evolved in dialogue with these environmental changes, which rewarded behavioral flexibility to negotiate heterogeneous, contingent environments. Human food production systems also reflect the importance of flexibility in the face of contingency. These adaptive responses are value-neutral, in that an adaptive response to the rise of an illicit ivory trade might run counter to environmental conservation. Indeed, the impacts of humans on megafauna have been dramatic,

even if relatively less in Africa than on other continents, and a consequence of continued defaunation would be a simplification of ecosystem structure and function. Moreover, recognizing that people in Africa have devised ways of managing adversity is not to suggest that Africans are free of or inured to suffering. It is to suggest that Africans' depiction as helpless and responding passively to world events is wrong—and that African-indigenous approaches have something to teach us all (4, 167). Again, humans are not an undifferentiated mass. Many of the most dramatic human impacts on environments have come during the past 500 years, since the beginning of imperialism in Africa. Africans have developed social systems capable of navigating the imperial world, although these strategies will be put to the test in a warmer, drier, and more densely populated Africa.

The above discussion demonstrates the importance of recognizing both the global implications of the Anthropocene as well as its specific, local manifestations. These so-called local Anthropocenes are shaped by biogeographic legacies and histories of disturbance both shallow and deep—and they are received with reference to their specific histories of conquest and (de)humanization, an understanding of which is critical to addressing environmental challenges. Using African experience to think about what it means to be human does not mean that Africa is a source of timeless wisdom, but rather that it has been a site of innovation about which we should know more. Progressivist, cumulative models of human social "development" implied that African society had lagged behind other regions, because African societies did not follow patterns of domestication and state formation familiar to Eurasian contexts (11, 12). This failure to question the assumptions of our models of human social change reflects the need for nuanced, *longue durée* accounts of how climate and other natural processes have textured human settlement and culture, as well as how and when specific humans have impacted those processes.

The Anthropocene raises an array of challenges for which we are ill-equipped with conceptual and practical tools, and African strategies might be instructive of the kinds of flexibility and adaptability needed to navigate our future world. But we also recognize the profound and unprecedented nature of Anthropocene conditions, and the questions this raises regarding the efficaciousness of African strategies. Climate changes in the coming century are likely to be dramatically different than those humans have experienced before, and the near quadrupling of the human population in Africa by 2100 poses tremendous challenges to states seeking to control or provide services to their citizenry (see also 5). Current political economic structures present another important set of challenges. Efforts to promote "development" in Africa have in many cases ignored the existence of flexible foodways and prevailing ecological conditions, leading to project failure and even environmental degradation (e.g., 166, 171). Although the expropriation of African resources has been justified on the notion that they are underutilized (181), the importance of flexibility to African foodways such as shifting cultivation and transhumance demonstrates that lands not continuously under production can be crucial to a system of production (176). Flexibility is all the more important in light of the difficulty of predicting the response of vegetation to changes in climate and disturbance regimes, given the tendency of abrupt shifts between forest and grassland in Africa's rainfall- and disturbance-driven ecosystems (18) and the potential for feedbacks between climate and land-cover change (49).

In addressing these challenges, we who care about African environments must find ways to conceive of both the long- and short-term, the local and global, and the ecological and social processes at work. Obtaining a better understanding of the societal and ecological mechanisms driving current and potential future environmental dynamics in Africa will be crucial to safeguard the continent's magnificent, but pressured natural heritage, and promote human livelihoods in the face of the ongoing strong demographic and multinational corporate expansion. Thinking with African environmental histories ultimately teaches us about how we might conceive of humans and their role in our multispecies world. Are we Earth stewards, charged with regulating ecological

processes? Or are we adaptive responders, making the most of contingent opportunities? The former suggests a degree of control we may not possess, even though it justifiably acknowledges the human role in producing the environmental crises now underway and our responsibility to address them. Perhaps the latter offers a more productive view. Perhaps we are contingent, opportunistic, adaptive responders, no doubt with an outsized environmental impact, but in dialogue with and "response-able" (31) to the world around.

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Errata

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