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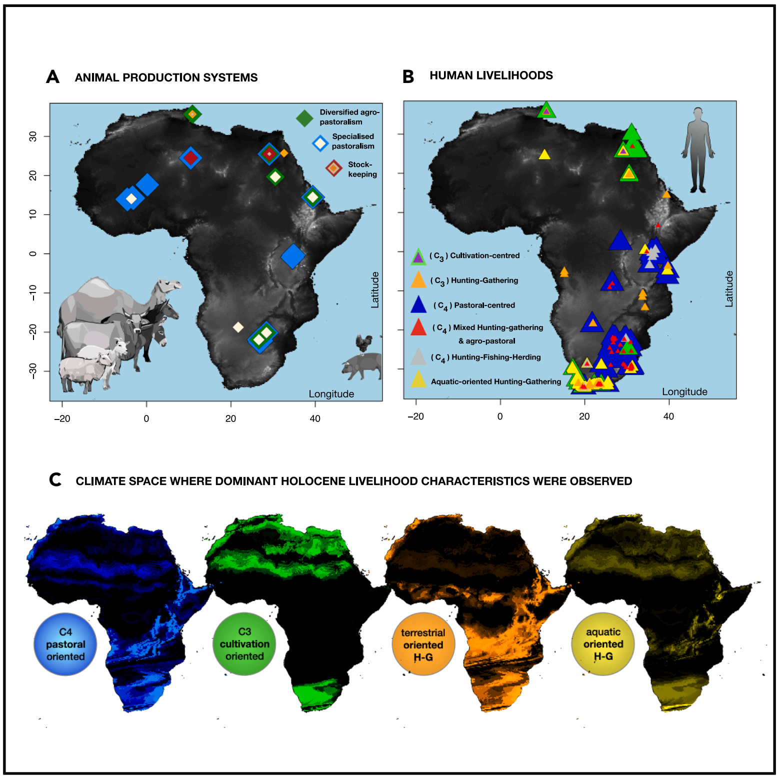
Africa-wide diversification of livelihood strategies: Isotopic insights into Holocene human adaptations to climate change

Graphical abstract



Highlights

- Livelihood diversification co-evolved with Holocene climate change across Africa
- C_3 and C_4 food-production strategies followed distinct spatiotemporal pathways
- The breadth and variability of pastoral livelihoods suggests a central adaptive role
- We offer a continental-scale reference for understanding Holocene livelihoods

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In brief

How did ancient African societies adapt to shifting climates? This study reveals that livelihood diversification—custom blends of pastoralism, cultivation, fishing, and foraging—was key to long-term resilience over the past 11,000 years. By analyzing archaeological, isotopic, and ecological data across the African continent, we show how communities navigated environmental change. These findings offer crucial insights for policy and adaptation planning today and highlight the importance of flexible, diverse livelihood strategies in sustaining societies amid intensifying environmental challenges.

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Africa-wide diversification of livelihood strategies: Isotopic insights into Holocene human adaptations to climate change

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SCIENCE FOR SOCIETY For thousands of years, African societies have adapted their livelihoods with shifting climates, yet current research lacks a comprehensive understanding of how these adaptations shaped long-term resilience. This gap limits efforts to support communities facing today's climate challenges. Our study examines how African livelihoods evolved over the past 11,000 years, using isotopic, archaeological, and ecological data to reveal patterns across different food-producing and foraging strategies. We show that livelihood diversification—combining pastoralism, cultivation, fishing, and gathering—was key to resilience. These findings offer valuable insights for policymakers, landscape managers, and adaptation planners by highlighting the role of livelihood diversification in sustaining communities amid environmental change. Understanding past responses to climate shifts can inform current and future strategies for building resilience in regions facing growing socio-environmental pressures.

SUMMARY

Sustainability challenges are intensifying across the globe and disproportionately impacting people, landscapes, and seascapes on the front lines of climate change. In particular, African communities, who contribute least to global climate change, bear the greatest burden of its impacts. Despite the African continent having the longest record of human-climate co-evolution globally, current research lacks an empirical continent-wide understanding of how Holocene livelihoods evolved to shape resilience today. To fill this gap, we analyze the archaeological and ecological context of isotopic niches (c. 11,000 BP to the present), to illustrate how adaptive strategies evolved during major climatic shifts (African Humid Period: c. 14,700–5,500 BP). We characterize Holocene livelihoods—pastoralism, cultivation, hunting-gathering, and fishing—to offer a continent-wide reference and to identify the spatiotemporal diversification patterns underpinning adaptation. This reconstruction offers critical insights into the mechanisms that shape resilience, with direct relevance for policymakers and practitioners working across climate adaptation, food security, and human well-being.

INTRODUCTION

Climate change is accelerating the frequency and intensity of environmental disturbances, posing profound challenges to livelihood resilience, food security, and human well-being worldwide. While these impacts are global, they are not evenly distributed—communities on the front line of climate change, particularly across Africa, are among the most impacted. Despite contributing minimally to anthropogenic climate change, African societies face disproportionate risks due to increasing climate variability and socio-ecological pressures.[1] As the impacts of climate change intensify, understanding how societies adapt to environmental change is critical for informing effective adaptation strategies that enhance contemporary resilience. However, a key knowledge gap remains in understanding how livelihoods and associated adaptation strategies co-evolve with shifting environmental conditions, particularly the complex and dynamic spatiotemporal evolution of different livelihood strategies in relation to Holocene climate change.[2,3] In part, this knowledge gap is due to a lack of continental-scale land use and land cover change datasets (although for pastoralism and pollen-derived vegetation datasets, see Phelps et al.[2–5]), as well as long-standing challenges associated with documenting food-gathering strategies and characterizing their complex spatiotemporal interactions with food-producing strategies.[6–13] As a result, the evolution of livelihood strategies has received relatively little attention, despite its central importance to understanding human adaptation and resilience.

The African Humid Period (AHP: c. 14,700–5,500 BP) was an interval of relatively wet conditions across much of Africa, driven by interactions between the West African summer monsoon and orbital forcing.[14–19] The AHP was characterized by spatiotemporal variability in hydroclimatic conditions, continental-scale changes in the extent and patterns of vegetation and aquatic ecosystems, and an expanded footprint of human occupation.[2,15,18,20–23] Following a decline in northern hemisphere summer insolation c. 11,000–9,000 BP,[24] the second half of the AHP was marked by major and rapid changes in human demography,[20,25] particularly during the time-transgressive termination of the AHP (c. 5,500–3,500 BP).[22] This study aims to fill a critical gap in understanding how African livelihoods evolved in relation to these shifting climate conditions during the AHP.

Pastoralist livelihood strategies in particular have long been considered as essential for adapting to unpredictable environmental conditions.[26–29] It has long been thought that African animal husbandry began c. 9,000–7,000 BP in unstable, marginal Saharan environments, where access to dietary resources was unpredictable.[30] However, changes in local land use were complex, with various potential routes to the incorporation of food-producing economies in northeast Africa, c. 9,000–7,000 BP.[31] Toward the end of the AHP, a southward shift of the Saharan desert margin was associated with a gradual exodus of people from northern Africa.[25] The spread of pastoralism across sub-Saharan Africa is well documented from c. 5,500 BP with drying climate conditions (i.e., at the termination of the AHP) and included complex interactions between food-gatherers and food-producers.[7,9,11,12,30,32,33] Beginning in eastern Africa, the sub-Saharan spread of animal husbandry occurred in mosaics or multiple events, and—unlike many other regions globally—broadly preceded crops.[30] This spread also reflected niche construction processes and involved complex interactions among pastoralists and hunter-gatherer-foragers.[3,11,34–37] The expansion of livestock prior to crops in Africa contrasts with other regions globally, where the spread of crops often precedes livestock.[30,38]

Stable carbon and nitrogen isotope analysis facilitates reconstruction of past human and faunal diets and habitat.[39–41] In particular, stable carbon isotope values ($\delta^{13}C$) from consumer tissues (i.e., biological material obtained from organisms that consume plants or other organisms, such as bones, teeth, or other organic matter) help to distinguish whether the individual is part of a food web based on C_3 versus C_4/crassulacean acid metabolism (CAM) plants (Figure 1). C_4 plants occur primarily in open ecosystems, whereas C_3 plants occur across closed (forest and thicket) and open (grass- and shrub-dominated) ecosystems and many heavily cultivated areas. Changes in consumer stable nitrogen isotope values ($\delta^{15}N$) can reflect a variety of changes in diet (e.g., shifts between plant, animal, aquatic foods, and trophic levels,[42] and habitat (e.g., soil N cycling, which is influenced by moisture availability, temperature, substrate type, and so forth). Provided there is high variation in consumer $\delta^{13}C$ and $\delta^{15}N$ values, complementary lines of dietary and environmental inference are needed to interpret isotopic signatures.

Generally, consumer tissues enriched in ^{13}C ($\delta^{13}C > -15‰$) reflect diets based on C_4/CAM plant food webs, potentially resulting from consumption of plant foods such as maize, sorghum, teff, African millets, and edible succulents, and animal products derived from tropical pasture grasses. Conversely, consumer tissues relatively depleted in ^{13}C ($\delta^{13}C \sim < -15‰$) reflect diets oriented toward (direct or indirect) consumption of C_3 plants, including plant foods such as wheat, rice, nuts, most vegetables and fruits, and products derived from animals that consumed shrubs and trees.[39,44] Aquatic-oriented animals and their consumers tend to be relatively enriched in ^{15}N and with $\delta^{13}C$ values similar to terrestrial grazers.[39,45,46] Consumer tissues become enriched in ^{15}N at higher trophic levels[42] and as a result of soil N cycling in hot and dry or manured environments.[40,47–51] In contrast, consumer tissues depleted in ^{15}N can reflect a relatively low trophic-level diet or soil N cycling in cooler and wetter environments, or without crop manuring.[39,44,52–56]

Livelihoods are a means of living and comprise a range of subsistence (or land/sea use) strategies, traditionally including four main types that occur on a continuum: pastoralism, cultivation, hunting-gathering, and fishing (Figure 2).[57,58] Livelihood strategies can center on one or more types of subsistence and include diverse combinations and relative proportions. The livelihoods framework is flexible enough to capture the reality of land-use ecology, as boundaries between subsistence categories are often flexible and dynamic, depending upon socio-ecological context. For example, animal production and cultivation often occur simultaneously within agricultural livelihoods,[58,59] and can be mixed with hunting-gathering and/or fishing.[10,12] Furthermore, the flexibility of the livelihoods framework is ideal for interdisciplinary studies spanning different spatiotemporal scales and data types, and allows explicit consideration of land use.[58] Characterization of livelihoods at continental scale allows for an enhanced understanding of human-climate-vegetation interactions and provides insight about how resilience strategies evolved in the past, informing current and future approaches to adaptation, resilience, and predictions of ecosystem change. However, such a continental-scale characterization and comparison of livelihoods does not currently exist for Holocene Africa.

Here, we address this knowledge gap by empirically defining human isotopic niches and their dominant Holocene livelihood

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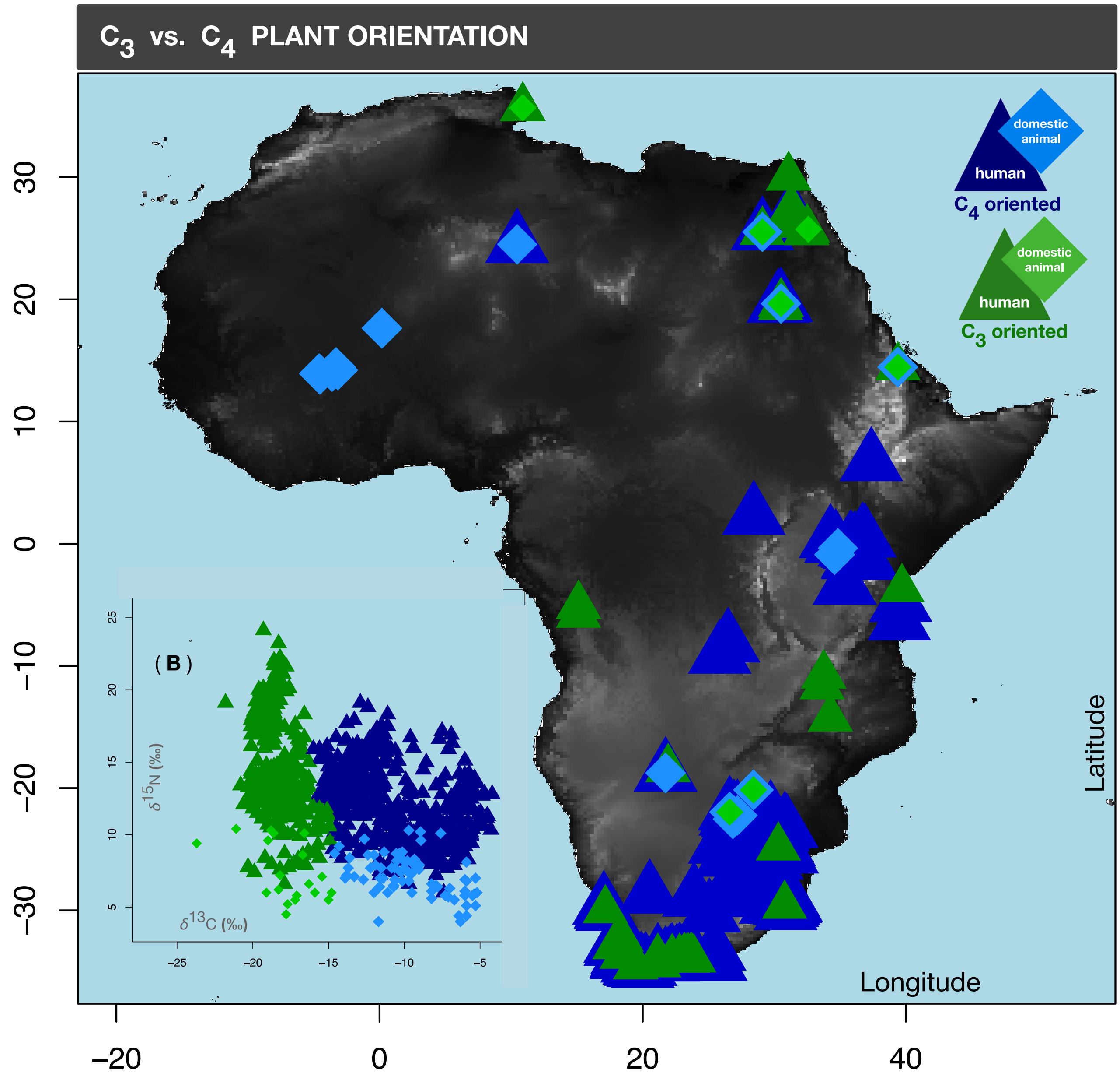

Figure 1. Distribution of human and domestic faunal isotopes oriented toward either the C_3 or C_4/CAM photosynthetic pathway

Samples are distributed using hierarchical clustering ($n = 2$). (A) Geographic distribution; (B) isotopic distribution. Both C_3 and C_4 plants have global distributions, but with C_4 plants dominating in warm, seasonally dry climates (e.g., C_4 savannas[43]) and tending to be restricted from dense forests and mountain tops.

characteristics on the African continent (i.e., including pastoralism, cultivation, hunting, and fishing). For supplementary comparison, we also empirically define domesticate isotopic niches and their animal production characteristics and compare these to the human isotopic niches. We then explore the spatiotemporal co-evolution of human and domesticate isotopic niches in continental Africa. In doing this, we address the overarching research question: as food production expanded on the African continent during a period of major climatic change (AHP: c. 14,700–5,500 BP), how did livelihoods evolve spatially and temporally, and what does this reveal about long-term socio-ecological adaptation and resilience to climate change? We established a continental-wide reference for African livelihoods and demonstrated the central role of livelihood diversification in shaping livelihood resilience to Holocene environmental change. By examining changes in Holocene livelihoods this way, we contribute an improved understanding of how people have adapted their land-use strategies over millennia of climate change at continental scale through diversification strategies. This study can inform contemporary issues around food insecurity and human well-being by demonstrating the different ways in which livelihood strategies can enhance or

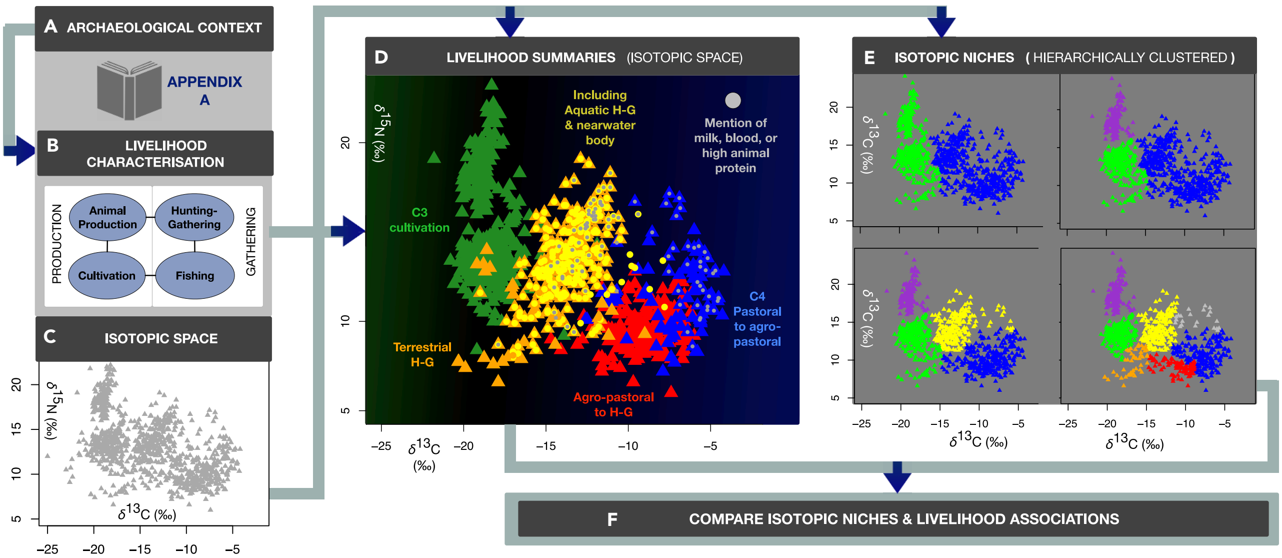

Figure 2. Establishing isotopic niches and their livelihood associations

(A) Collate subsistence information from site-based archaeological context.[60]

(B) Establish a livelihood characterization scheme for Holocene Africa by interpreting contextual archaeological information within a livelihoods framework (i.e., dominant combinations of cultivation, pastoralism, hunting-gathering, and fishing).

(C) Process and plot isotopic records in isotopic space.

(D) Plot livelihood summaries in isotopic space using the livelihood characterization scheme.

(E) Define isotopic niches using hierarchical clustering.

(F) Combine livelihood summaries and isotopic niches to determine livelihood associations for each isotopic niche.

diminish societal resilience to climate change and shifting environmental conditions—especially in regions that are most impacted by climate change.

RESULTS AND DISCUSSION

Methods summary

We first define the isotopic niches of people and their domestic fauna using hierarchical clustering of bone collagen δ^{13}C and δ^{15}N data,[61] i.e., human bone carbon and nitrogen isotopes, domesticate bone carbon and nitrogen isotopes, and enamel carbon isotopes, then summarize the livelihood characteristics of each niche with subsistence information from site-based archaeological context. For each niche and its defined livelihood characteristics, we then explore spatiotemporal patterns and trends and discuss their development in climatic and geographic context. Note that our study builds on the concept of the "isotopic niche" but does not aim to transform isotopic values into relative proportions of dietary resources using mixing models and isotopic baselines (e.g.,[62,63]). Instead, we employ methods that allow characterization of isotopic niches at continental scale with relatively limited data coverage, using livelihood, geographic, and climatic information (Figure 2).

Characterizing human livelihoods from isotopic niches

Human diets during the African Holocene were broadly split between primary reliance on C_3 plants (57%: δ^{13}C from −15‰ to −22‰) or C_4 plants (43%: δ^{13}C from −4‰ to −16‰) (Figure 1), whether consumed directly from plants or indirectly from terrestrial and aquatic fauna. Although people were unlikely to be explicitly aware of C_3-C_4 differentiation, our study demonstrates that the C_3-C_4 split in livelihood strategies reflects differences in the ecological characteristics of plants consumed as part of different subsistence strategies: Both C_3 and C_4 plants have global distributions, but C_4 plants dominate in warm, seasonally dry climates (e.g., C_4 savannas[43]) and tend to be restricted from dense forests and mountain tops.

Most C_3-oriented diets clustered into two related isotopic niches (green triangles and purple triangles: 38%), which reflect livelihoods centered on C_3 cultivation (Figure 3). Most C_4-oriented diets were clustered into two isotopic niches (blue triangles and red triangles: 32%), which reflected livelihoods centered on or depending upon C_4 pastoralism. Prior to the arrival of food-producing strategies (c. 9,000–7,000 BP in North Africa; c. 5,500 BP in sub-Saharan Africa; c. 2,000 BP in southern Africa), African livelihoods included diverse hunting-gathering strategies (Figure 3A), which tended toward either mixed C_3/C_4 diets with limited reliance on ^{15}N-enriched proteins (orange triangles) or mixed C_4/C_3 diets with substantial reliance on ^{15}N-enriched proteins (i.e., including aquatic protein: yellow triangles). With the spread of domesticated plants and animals, diets expanded to include more polarized dependence on C_3- and C_4-oriented livelihood strategies, including: C_3-centered agriculture (green triangles and purple triangles), C_4-centered pastoralism and agro-pastoralism (blue triangles), agro-pastoralism with hunting-gathering (red triangles), and mixed hunting-herding-fishing strategies (gray triangles).

Livelihoods reliant on pastoralism occurred across the largest number of archaeological sites (61%), while those reliant on

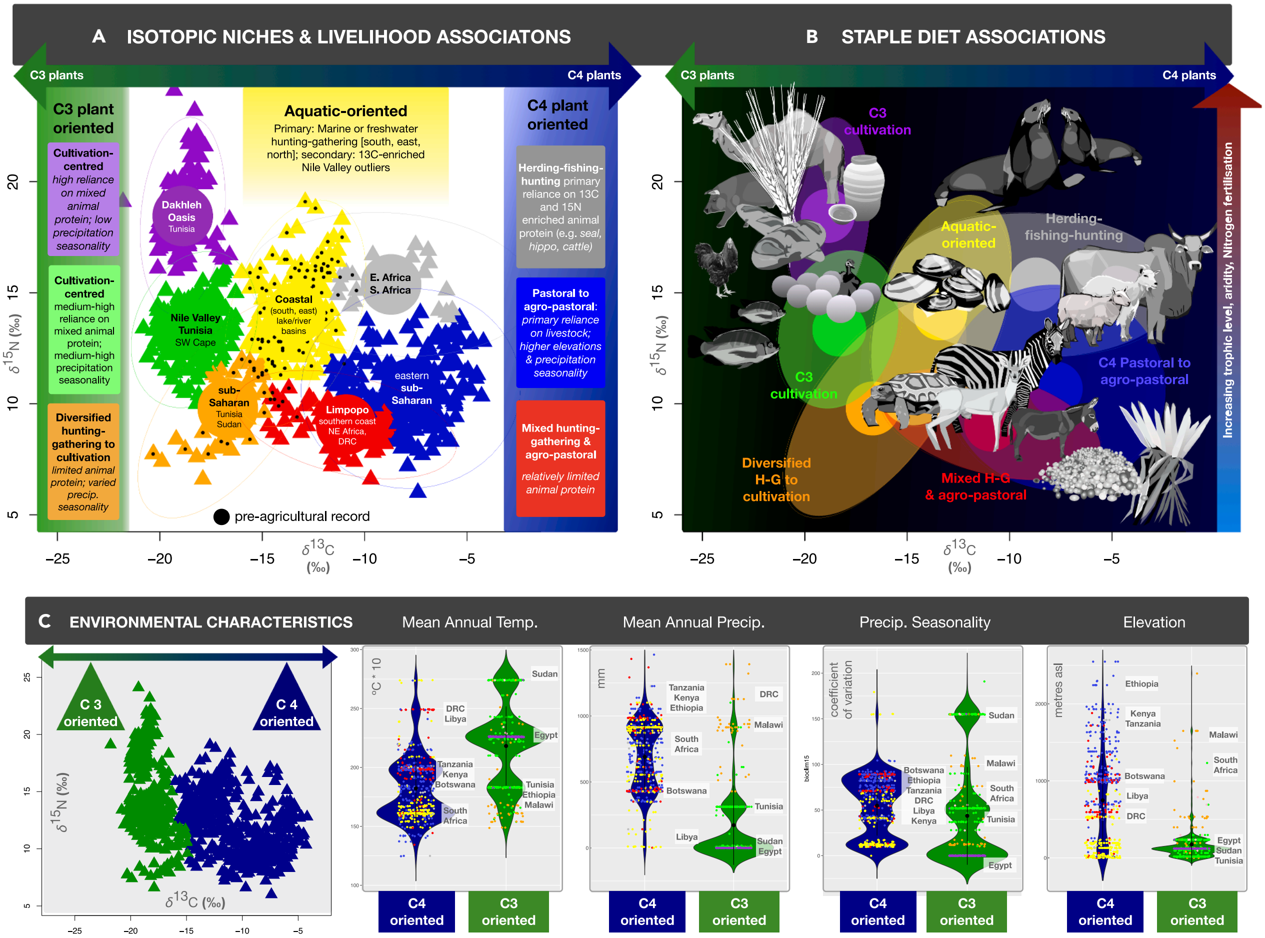

Figure 3. Characteristics of Holocene livelihoods from isotopic niches (human bone collagen)

(A) Livelihood descriptions and regional distributions associated with each isotopic niche. For comparison of livelihood context and isotopic niches and the temporal development of isotopic niches, see Figures S1–S4.

(B) Diet staples associated with isotopic niches. Data ellipses have a confidence level of 98%.

C_3 crops occurred across the fewest (12%). Pastoral-reliant livelihoods also demonstrated the highest $\delta^{13}C$ variation (coefficient of variation [CV] ~26) and the second highest variation in $\delta^{15}N$ values (CV ~15, after diversification ~16), reflecting the adaptability of pastoral livelihoods to a range of vegetation, climate, elevation, and dietary conditions across the continent (Figures 4, S1, and S2). Livelihoods centered on C_3 cultivation spanned a wide range of seasonal conditions, but were relatively restricted to low precipitation and elevation environments (Figures 3 and S5). The ubiquity and variability of pastoral livelihoods suggests that they were central to Holocene resilience across the continent, whether through adaptation to variable environmental conditions or livelihood diversification in the face of climatic change.

Two groups of C_3-oriented livelihoods were identified. The first group primarily includes cultivation-centered livelihoods with ^{15}N-enriched animal proteins, occurring in Egypt, Sudan, and Tunisia c. 7,000–1,400 BP (purple triangles and green triangles, n = 338). The second group primarily includes C_3-oriented sub-Saharan hunter-gatherer-foragers with minimal $\delta^{15}N$-enriched animal protein (orange triangles, n = 49), occurring earliest in coastal South Africa (c. 10,500 BP in South Africa, c. 8,000–2,500 BP in Malawi, c. 2,500 BP in Ethiopia, c. 1,300–1,000 BP in Xaro, and from c. 500 BP in Democratic Republic of the Congo [DRC] and Kenya).

C_3 cultivation-centered livelihoods with ^{15}N-enriched animal protein (green triangles and purple triangles) include diverse, C_3-centered cultivation ($\delta^{13}C$: ~ −22‰ to −16‰) in the relatively dry, hot climates of Egypt, Tunisia, and northern Sudan (~0–300 mm/year). Dietary staples include C_3 crops, such as emmer wheat and barley for bread and beer, fruits, legumes, and flax (e.g.,[64–68]). These livelihoods also include reliance on ^{15}N-enriched animal products, such as aquatic resources (e.g., freshwater fish, fish sauces, dried fish, and fish cakes/balls[64,69]), livestock products from stock-keeping and agro-pastoralism (e.g., eggs, milk, meat, and dung), and possible contributions from specialized pastoralist systems (e.g., specialized camel pastoralism in Egypt; cattle pastoralism in Sudan). The purple-triangle subtype primarily occurs at Kellis (Egypt) and involves a very similar variety of foods to the green-triangle subtype (e.g.,[64]), but it is associated with lower average precipitation and a more specialized, ^{15}N-enriched

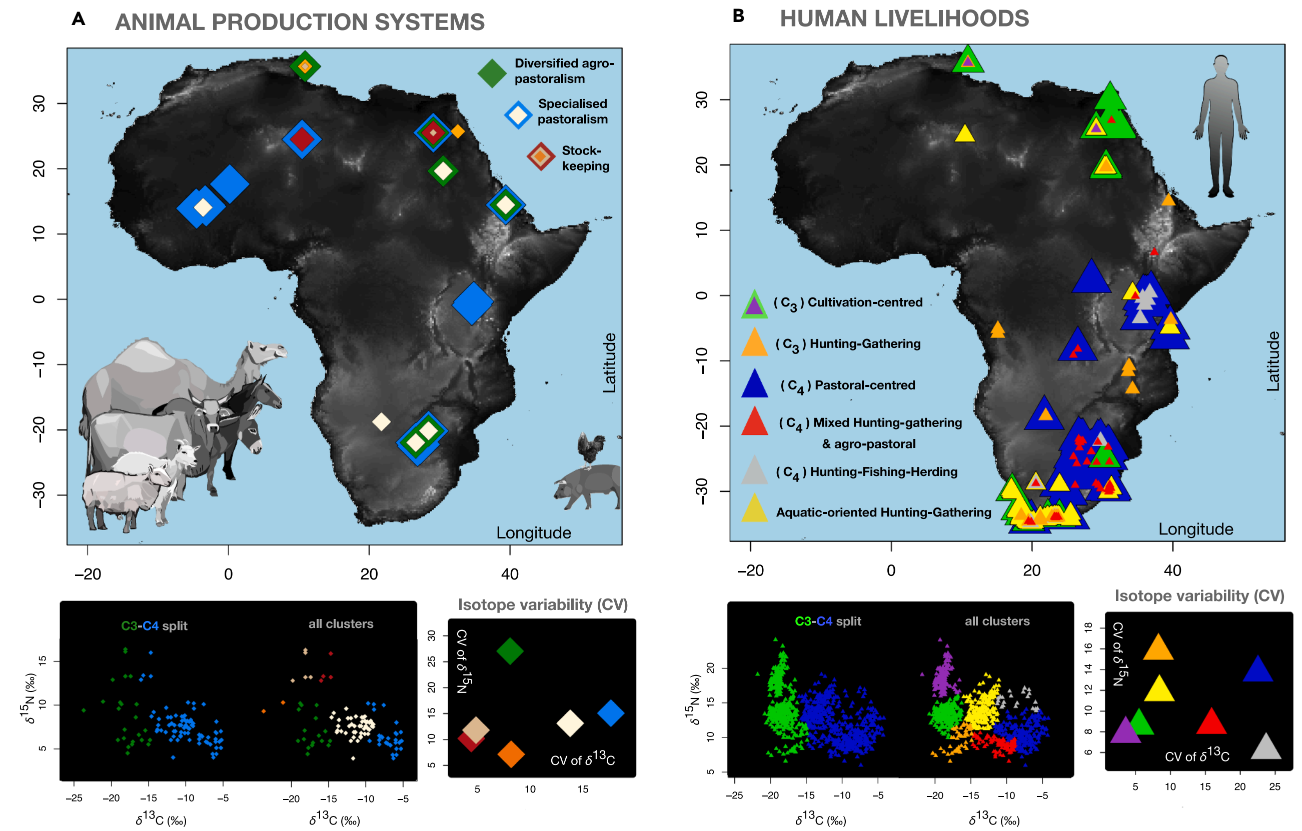

Figure 4. Geographic and isotopic characteristics of Holocene livelihoods

(A) Characteristics of animal production systems: geographical distribution based on bone and enamel isotopes (top); isotopic niches (bottom left); isotopic variability (coefficient of variation (CV): and the standard deviation divided by the mean × 100) of each niche (bottom right). These records are indicated by diamonds.

(B) Characteristics of human livelihoods: geographical distribution based on bone isotopes (top); isotopic niches (bottom left); and isotopic variability of each niche (bottom right). These records are indicated by triangles. For comparison of environmental characteristics between animal production systems and human livelihoods and between C_3- and C_4-oriented systems, see Figure S6.

diet (purple triangles: CV of δ^{13}C 3.6, CV of δ^{15}N 7.8; green triangles: CV of δ^{13}C 5.4, CV of δ^{15}N 8.5). However, provided the wide breadth of δ^{15}N values in human diets at Kellis c. 2,400–1,500 BP (δ^{15}N: ~ +13‰ to +24‰; Figure S7) and the higher variation in δ^{15}N than δ^{13}C values, this pattern may reflect a combination of soil aridity and/or agricultural practices(e.g., crop manuring[39,44,52–56,68]), which result in ^{15}N enrichment of human and small-stock diets (e.g., pig, chicken, goat, and donkey).

A small portion of the green-triangle cluster (3%; n = 10) also includes mid to late Holocene hunter-gatherer outliers on the southwestern Cape (~100–1,000+ mm/year), with similar isotopic characteristics to cultivation-centered livelihoods. These outliers likely include coastal hunter-gatherers with relatively high reliance on terrestrial foods,[70,71] i.e., depleted ^{13}C compared to other individuals at the same sites (e.g., Somnas, Zitzikama, and Melkbosstrand), due to higher incorporation of wild or domestic C_3 plants or C_3-dependent fauna. However, one of these outliers occurred in the Limpopo Basin (northeast South Africa) during the late Holocene, and is difficult to interpret because it involves an isolated child,[72] potentially affected by breastfeeding or weaning.

C_3 hunting-gathering livelihoods with minimal ^{15}N-enriched animal protein primarily occurred throughout the Holocene in sub-Saharan Africa (orange triangles: n = 43) across a wide range of environments (Figures S5 and S6). Dietary information for these livelihoods is limited, but the majority may be associated with southern African San ancestry,[73] identified on the southern coast during the Early Holocene, in Malawi c. 8,000–2,500 BP, Ethiopia c. 2,500 BP, northern Botswana c. 1,500–1,000 BP, and Kenya and western DRC c. 400 BP. Dietary composition likely varies widely depending upon the environment, but these livelihoods are often plant centered with limited input from ^{15}N-enriched animal proteins (e.g., 70%:30% for Botswanan San[74]). At Chencherere in Malawi, for example, resources are suggested to include a wide variety of foraged foods, such as fruits, leaves, flowers, tubers/roots, seeds, mushrooms, gourds, nuts, honey, barks, medicinal roots, and some trapped or hunted wild fauna (e.g., zebra, duiker, wildebeest, reedbuck, klipspringer, hartebeest, and warthog)[60]. These livelihoods are ^{15}N depleted relative to hunter-gatherers at similar precipitation levels on the southwestern Cape and have δ^{15}N values only slightly enriched relative to associated domestic and wild fauna (Figure S9). Like the red cluster, these livelihoods may incorporate some agriculture.

A small portion of this group (orange triangles: n = 6) includes outliers from cultivation-dominated livelihoods in Sudan c. 6,500–6,000 BP and Tunisia c. 1,700–1,400 BP, with depleted ^{15}N (d^{15}N: ~ +8‰ to +12‰) relative to other people at the same sites. This may reflect incorporation of more wild foods into these diets, or it may reflect outlier diets with limited faunal consumption.

C_4-oriented livelihoods

Four main groups were identified among C_4-oriented livelihoods, namely those centered on pastoralism (blue triangles: n = 201), diversified hunting-gathering with aquatic protein (yellow triangles: n = 208), mixed hunting-gathering and agro-pastoralism (red triangles: n = 97), and intensive herding-hunting (gray: n = 23).

Pastoral-centered livelihoods (n = 201) span a broad range of present-day environmental conditions (~300–1,900 mm/year) and include a range of dependence on pastoralism, agro-pastoralism, and some hunting-gathering (blue triangles). Pastoral-centered livelihoods are associated with strong reliance on C_4 plants (δ^{13}C: −15‰ to −5‰) and typically include a staple dietary combination of variable pastoral products and C_4 crops (e.g., meat, milk, blood, millet, and sorghum[75,39,76–79]). The isotopic signatures of pastoral livelihoods are associated with the Pastoral Neolithic, Elmenteitan Neolithic, and South African Iron Age, and overlap with Kalenjin diets, which were identified as relying on C_4 grain and cattle/caprine pastoralism.[39] While these livelihoods cover a broad range of environments, they were restricted to sites where present-day precipitation is greater than ~300 mm/year and relatively seasonal (Figures 3 and S6). On the southern coast, one mid-Holocene outlier occurred, but due to its insecure age range (Sea View: c. 6,000–2,100 BP), it may have been an early herder rather than a true outlier.

For livelihoods occurring near or after the time of domesticate introductions, it is difficult to ensure that they do not reflect outlier hunter-gatherer diets (e.g., Matangai Turu Northwest in DRC, Prettejohn's Gully, Naishi Rockshelter, Diamant, and Sea View). However, provided that no livelihoods were securely misassigned prior to domesticate introductions and that the pastoral and aquatic-oriented clusters are well differentiated at mid to high δ^{15}N values, it is likely that most individuals are not aquatic-oriented outliers.

Mixed hunting-gathering and (agro-)pastoral livelihoods (n = 90) occurred across a similar range of environments to pastoralist-centered livelihoods, albeit at lower elevations on average (red triangles: Figures 3, S5, and S6). These livelihoods include highly variable reliance on agro-pastoralism and hunting-gathering and primarily occurred in South Africa, Botswana, and DRC following the spread of livestock to southern Africa (c. 2,000 BP). Two individuals with overlapping isotopic signatures also occurred in Egypt (c. 4,000 BP) and Kenya (c. 1,800 BP), the latter of which is associated with Luyia and Kikuyu livelihoods and described as having mixed C_4-C_3 cultivation with small amounts of pastoralism.[39]

This group also includes a small portion of early to mid-Holocene hunter-gatherers from coastal South Africa (n = 7). These livelihoods had similar isotopic characteristics to C_3-oriented hunting-gathering (orange triangles) and likely relied on similar diets with a higher C_4 component (e.g., grazing animals such as antelope and buffalo or low-trophic-level C_4 aquatic foods). Some late Holocene livelihoods likely also incorporated large components of hunting-gathering.

Hunting-fishing-herding livelihoods (n = 23) are the least common and occur across a wide range of present-day environments (~100–1,200 mm/year). These livelihoods are associated with strong dietary reliance on fauna and C_4-oriented diets (e.g., cattle, buffalo, hippopotamus, seal, and other C_4-oriented antelopes or aquatic resources) and likely include a mix of terrestrial and aquatic fauna with ^{15}N-enriched diets.

Ten of the individuals reflecting hunting-herding-fishing livelihoods lived during the early Holocene in coastal South Africa and were among the least ^{13}C enriched of the group, likely due to high reliance on marine resources. Seven of these ten individuals were from coastal sites (c. 11,000 BP to recent times), likely including specialized diets with large components of high-trophic-level marine protein and potentially some terrestrial hunting (e.g., seal, carnivorous fish, grazing shellfish, hippo, buffalo, and antelope[46,56,80,81]). Two of the remaining individuals were from the Orange River Basin (c. 400–100 BP) and likely practiced specialized hunting-herding (e.g., Namneiqua relying on cattle and wild resources such as rhino, hippopotamus, buffalo, and fish[82]). The final individual, from the Limpopo Basin (Skutwater), was associated with reliance on both herding and hunting.[83]

The 13 remaining individuals from the hunting-herding-fishing group (the most ^{13}C enriched) are associated with specialized pastoralism in the East African Plains, with high reliance on animal proteins that likely include both domestic and wild fauna. These livelihoods likely include diverse forms of herding-fishing-hunting strategies, and reflect the complex ancestry of pastoral neolithic and forager origins (e.g., Gishimangeda Cave[11]). Further supporting this, these hunting-fishing-herding livelihoods are more similar on average to aquatic-oriented livelihoods (yellow triangles) than pastoral-oriented livelihoods (blue and red triangles) and often co-occur with aquatic-oriented livelihoods near water bodies (e.g., Lake Eyasi, Lake Naivasha, Limpopo River, and Orange River). These results reflect the likelihood that complex hunting-fishing-herding strategies occurred across the continent, but are under-recognized.[10]

Aquatic-oriented hunting-gathering livelihoods (n = 208) occurred near water bodies and across a wide range of present-day environments (yellow triangles: ~0–1,700 mm/year). They are broadly ^{15}N enriched (δ^{15}N: ~ +11‰ to +19‰), likely due to diets including ^{15}N-enriched marine or freshwater resources, and they involve a diversity of aquatic/terrestrial hunting-gathering strategies (δ^{13}C: ~ −16‰ to −11‰), which were most common in coastal South Africa (n = 192[46,72,84]). Aquatic-oriented livelihoods in other locations had overlapping characteristics to those in coastal South Africa, including at Lake Victoria c. 3,500 BP, Lake Chad Basin c. 7,000–6,000 BP, coastal Tanzania c. 1,500–1,000 BP, and the Orange River Basin c. 400 BP. There was no clear differentiation between ^{15}N-enriched individuals in coastal or freshwater areas. It is likely that this group includes some fisher-herders or fisher-hunters, consistent with evidence from East Africa that herders co-occurred with fishers and often had dynamic herder-fisher relationships.[10,12,85] Furthermore, four individuals from the Orange River Basin (c. 400

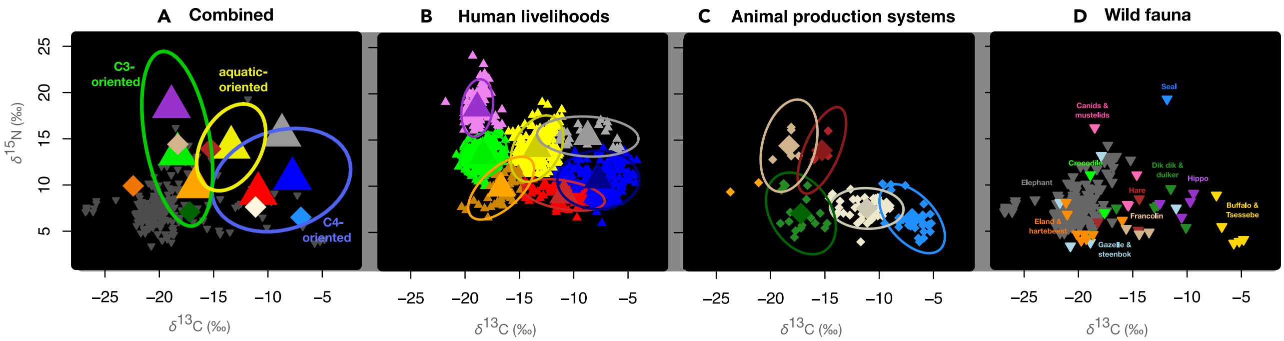

Figure 5. Comparative isotopic relationships between human livelihoods, animal production systems, and wild fauna

(A) Summarized relationships between animal production systems, human livelihoods, and wild fauna. Animal production systems oriented ~3‰–5‰ beneath livelihoods may reflect that domesticates are making substantial contributions via milk or meat products to the diets of people with associated human livelihood strategies,[42,88] e.g., specialized pastoralism (blue diamonds, white diamonds) contributions to pastoral livelihoods (blue triangle), and agro-pastoral (green diamonds) and stock-keeping contributions (orange, red, and tan diamonds) to different C_3-oriented livelihoods (purple, green, and orange triangles). Data ellipses have a confidence level of 98% and reflect C_3-oriented, C_4-oriented, and aquatic-oriented systems.

(B) Human livelihoods. Data ellipses have a confidence level of 90%.

(C) Animal production systems. Data ellipses have a confidence level of 90%.

(D) Selected groups of wild fauna. For site-based comparisons, see Figure S9.

BP) were associated with mixed herding-hunting-fishing livelihoods,[82] with two of these falling into the aquatic-oriented cluster (yellow triangles) and two into the intensive herding-hunting cluster (gray triangles). While this may be an accurate reflection of complex herder-hunter-fisher dynamics in the region (e.g., mixed reliance on fish, hippo, and terrestrial fauna[82]), environmental variation makes it difficult to determine whether such livelihoods are precisely assigned. Similarly, complex herder-hunter-fisher dynamics may have occurred during the AHP in North Africa, e.g., in the Acacus Mountains where early fish-reliant hunter-gatherers and herders were identified (n = 3[86]), and along the Sudanese Nile (n = 8), where heavy reliance on aquatic resources was apparent prior to c. 5,000 BP.[87]

While we did not find any evidence to support this possibility, it is possible that non-aquatic herding or hunting livelihoods with ^{15}N-enriched and mid-range δ^{13}C diets could be misidentified here as aquatic oriented (see Griqua, Turkana, and Dasenech[39]; e.g., Takarkori Rock Shelter and Kakamas). Overall, however, individuals in the aquatic-oriented hunting-gathering livelihood niche are described as incorporating varied aquatic resources into their diets and are located next to water bodies[60] (Figure S1).

Contextualizing animal production systems

The isotopic niches of domestic faunal diets reflect six animal production systems (Figure 4), oriented either toward C_4 plants (85%: n = 141: blue, white, and red diamonds) or C_3 plants (15%: n = 24: green, orange, and tan diamonds). Both C_4- and C_3-oriented animal production systems occurred in similar environments, but C_4-oriented systems tended toward sites with higher precipitation seasonality, elevation, temperatures, and precipitation levels on average (Figure S6), and were more ubiquitous (sites: n = 21) than C_3-oriented systems (sites: n = 7). C_4-oriented systems were also associated with high cattle-to-caprine ratios (~70% cattle and ~30% caprines) compared to C_3-oriented ones (30% cattle and 70% caprines), with the latter including more reliance on other types of livestock in northern Africa (e.g., pig, chicken, dog, camel, and donkey: Table S2).

Most C_4-oriented animal production systems (blue diamonds and white diamonds: n = 132) demonstrated high variation in δ^{13}C values (CV of δ^{13}C, ~26; CV of δ^{15}N, ~19) and were closely coupled to isotopic variation in C_4-oriented pastoral livelihoods (blue, red, and gray triangles: CV of δ^{13}C, ~26; CV of δ^{15}N, ~19; Figures 4 and 5). However, a small portion of these were ^{15}N enriched (δ^{15}N: ~ +13‰ to +16‰), overlapped with aquatic-oriented livelihoods (yellow triangles, n = 4; Egypt, Libya), and had low variation in δ^{13}C (CV of δ^{13}C, ~4), suggesting a specialized stock-keeping diet with fish consumption.[86]

Unlike C_4-oriented systems, C_3-oriented animal production systems were associated with high variation in δ^{15}N (CV of δ^{13}C, ~11; CV of δ^{15}N, ~40) and were decoupled from isotopic variation in C_3-oriented human livelihoods (CV of δ^{13}C, ~6; CV of δ^{15}N, ~22; Figures 4 and 5). This indicates that C_4-oriented human livelihoods (blue, red, and gray triangles) were likely centered on specialized cattle-caprine pastoralism (blue diamonds and white diamonds), whereas C_3-oriented livelihoods likely involved contributions from different forms of animal production systems adapted to cultivation or hunting-gathering-centered livelihoods (e.g., agro-pastoral [green diamonds] or stock-keeping [orange diamonds and tan diamonds]).

Specialized (C_4) pastoralism (white diamonds and blue diamonds) occurred in environments where present-day precipitation seasonality is high (CV, ~155–90; e.g., Sudan and Mali) and/or landscapes were mountainous (~2,400–800 m: Ethiopian Highlands, Zimbabwe, Botswana, Acacus Mountains, and western Kenya; e.g., bimodal rainfall regime[89]), with the exception of specialized camel pastoralism, which was possible in environments with low-precipitation seasonality and elevation (e.g., Egypt[90]). Specialized pastoral systems were utilized, for example, near the end of the AHP (c. 4,500–3,000 BP) in the Acacus Mountains (e.g., emerging cattle-centered practices[91]), northern Ethiopian Highlands, and eastern Mali; c. 2,000 BP in western Kenya and Sahelian Mali, and from c. 1,000 BP onward in northern and eastern Botswana and southwestern Zimbabwe. Two pastoral subsystems comprise this category (white diamonds and blue diamonds), ranging from relatively low (white diamond $\delta^{13}C$, -15 to -9) to high (blue diamond $\delta^{13}C$, -10 to -5) reliance on C_4 plants. The subsystem with high reliance on C_4 grasses (blue diamonds) is associated with the highest overall proportions of cattle (>90% cattle and <10% caprine or donkey: Table S2), although herd composition varied by site, e.g., being largely caprine based at Bosutswe c. 1,000–700 BP. The subsystem with low reliance on C_4 grasses (white diamonds [seven clusters]) had a lower cattle-to-caprine ratio (~60% cattle and ~40% caprines: Table S2) and often includes donkeys, chickens, or horses.

Diversified (C_3) agro-pastoralism was adapted to a variety of livelihoods ($\delta^{15}N$: ~ +4‰ to +10‰; CV of $\delta^{15}N$, ~27; Figure S9) and tended to occur at lower elevations (~0–1,300 m) and precipitation seasonality (CV ~0–155) than specialized pastoralism (green diamonds). Diversified agro-pastoralism is also associated with relatively low cattle-to-caprine ratios (~25% cattle and ~75% caprines) and high incorporation of other livestock such as pigs, chickens, dogs, camels, and donkeys (Table S2). Examples of agro-pastoral systems include c. 6,000 BP in North Sudan (sheep and dog), Ethiopia c. 3,000 BP (chicken), c. 1,700 BP in Tunisia (cattle, caprine, and pig), c. 1,000 BP onward in eastern Botswana (cattle and caprine), c. 500 BP onward in western Zimbabwe, and more recently in central Egypt.

Stock-keeping strategies (orange, tan, and red diamonds) typically involve household husbandry of relatively few animals, which provide secondary animal products and risk-reduction strategies to support other subsistence practices.[58] The stock-keeping systems identified herein have relatively low isotopic variation (CV of $\delta^{13}C$, ~4 to 8; CV of $\delta^{15}N$, 7 to 12) and were likely adapted to a variety of livelihoods and associated diets, including those oriented toward C_3 cultivation (Figures 4 and 5: green and purple triangles), C_3 hunting-gathering (orange triangles), and aquatic resources (yellow triangles) (Figure S9). A variety of factors can influence the ^{15}N enrichment of stock-keeping domesticates and the people they support, including aridity,[50] consumption of ^{15}N-enriched animal protein by both people and domesticates,[75–77,86,92,93] and agricultural practices such as manuring.[48,50] Examples of analyzed stock-keeping practices include: c. 3,800 BP in Libya (sheep), from c. 1,600 BP in Egypt (caprine, cattle, chicken, pig, donkey, and camel), and c. 1,600 BP in Tunisia (sheep). Based on enamel isotopes, aquatic-oriented stock-keeping may have also occurred in Mali's Tilemsi Valley (c. 4,500 BP[79]) and by Lake Victoria in Kenya (c. 2,000–1,600 BP[94]); however, due to the inability to differentiate enamel records with ^{15}N, these records could alternatively reflect agro-pastoral or specialized pastoral practices.

Livelihood pathways and interactions

Spatiotemporal changes in human and domesticate isotopes reflect the development of African livelihoods in the face of Holocene environmental change. The spatiotemporal trajectory of pastoral-oriented livelihoods reflects the documented, complex spread of domestic animals from North Africa into sub-Saharan Africa,[3,11,30] largely initiating along the East African Rift. Holocene environments with specialized pastoral practices include those with relatively high precipitation seasonality and/or mountainous landscapes (e.g., the Sahel, Ethiopian Highlands, and East African Rift into eastern and southern Africa). During the mid-Holocene, specialized pastoral systems spread from highly seasonal Sahelian environments into high-elevation East African environments. Conversely, evidence for mid-Holocene pastoral systems in sub-Saharan West Africa is absent, likely explained by environments with both low-precipitation seasonality and elevation. In this sense, mountainous East African landscapes were likely better suited to the uptake of specialized pastoralism (i.e., cattle before crops[30]) than West Africa, offering explanatory support for only small-scale food production and scarce agricultural records in West Africa, for thousands of years after the AHP[95]; and despite evidence for crop domestication in the western Sahel[79,96–98]). Furthermore, these climatic and topographic differences between East and West Africa may also explain why trypanotolerant cattle breeds evolved in West Africa (e.g., N'Dama, Bambara shorthorn, and Baoule[99,100]).

In the northeast, a band of high-precipitation and low-precipitation seasonality in Ethiopia and southern Sudan may have also acted as an environmental barrier against the spread of specialized pastoral systems from North Africa into East Africa (e.g., posing disease challenges such as trypanosomiasis[100]). Drying during the end of the AHP may have reduced these climatic barriers over time, and the relatively early termination of the AHP in North Africa may have increased land-use pressures in the Sahel,[2,3,20,25] potentially driving a need for pastoral routes into sub-Saharan Africa, e.g., via expansion of pastoral livelihoods into the Ethiopian Highlands.[7] In this sense, the spread of specialized pastoralism into East Africa may have depended upon the navigation of complex mountainous landscapes and interactions with resident hunter-gatherers along the East African Rift.[9,11]

Spatiotemporal patterns also reflect the southern coast as a major center for hunting-gathering diversity, with aquatic and terrestrial-oriented strategies occurring from c. 11,000 BP onward.[46,72,84]. While aquatic-oriented hunting-gathering occurred across the southern coast during the early Holocene, terrestrial-oriented strategies were centered in the Plettenberg Bay area and likely spread northeast to Malawi and further north[73] as well as westward toward the western Cape (Figure 6). These Holocene pathways likely paved the way for the subsequent development of mixed pastoral, agro-pastoral, and hunting-gathering livelihoods in southeast Africa from c. 2,000 BP. Aquatic-oriented hunting-gathering livelihoods in East Africa are only represented herein from c. 3,500 BP (e.g., late Kansyore) but likely extended much earlier.[10,101]

Livelihood diversification occurred after c. 2,000 BP in southeastern Africa, possibly relating to both the southward migration of Bantu people[105] and the northward migration of San communities.[73,82] Particularly notable about this period in the Zambezi Basin, is the development of mixed food-gathering and food-producing strategies—including variable combinations of specialized pastoralism, agro-pastoralism, and hunting-gathering. Useful future research may investigate how the spread of hunter-gatherer livelihoods to Malawi c. 8,000 BP and further north[73] interacted with and influenced the development of pastoral-oriented livelihoods. Further investigation is needed to understand whether environmental conditions in southeastern Africa (e.g., low-precipitation seasonality)

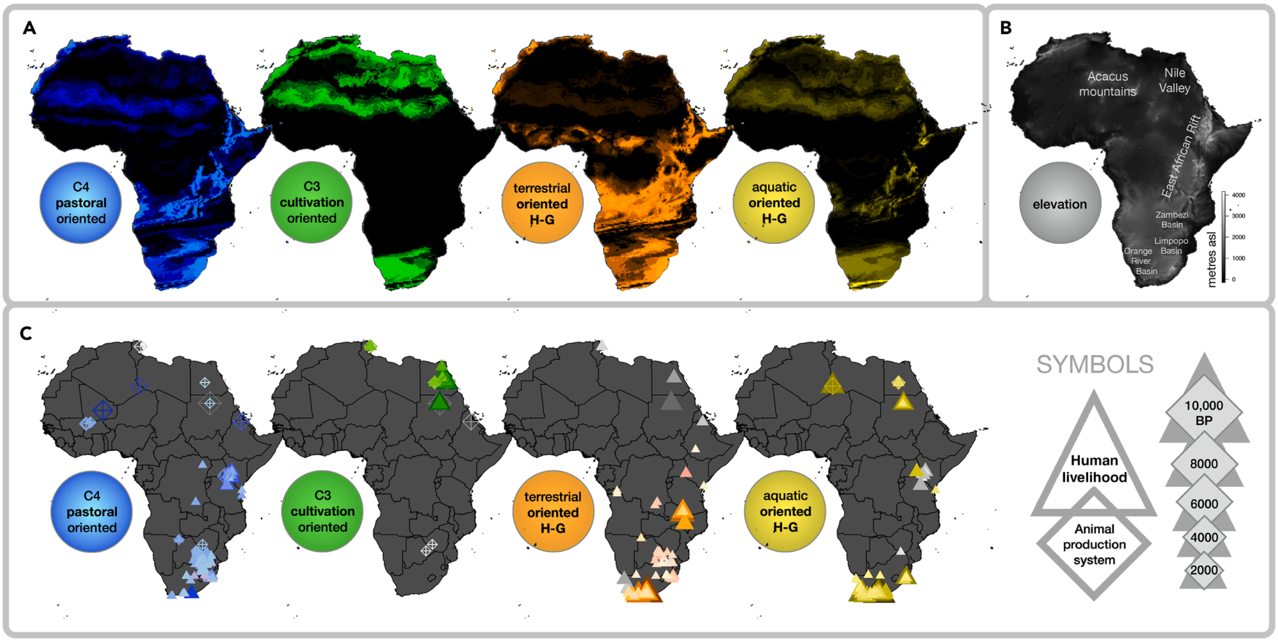

Figure 6. Spatiotemporal distribution of Holocene livelihood strategies

(A) Spatial projections of Holocene livelihood climatic niches. Reconstructions were done using human and domestic isotopes (point data in C), ordered by site-based archaeological context[60] and inferred using modern-day climate information (WorldClim v.2[102]). Niche dynamics reconstructions were done using the "ecospat" package in R (R Core Team[103,104]; for related methodology, see Phelps et al.[2,3]).

(B) Elevation map (meters asl) with key regional designations of relevance to the study.

(C) Spatiotemporal change in human livelihoods by isotope record, based on human bone (triangles) and domesticate bone and enamel (diamonds). Grayscale symbols indicate that a given livelihood may occur but is uncertain (e.g., a cluster outlier). Blue symbols: pastoral-oriented livelihoods are primarily indicated by C_4 pastoral-oriented livelihoods and animal production systems; possible secondary indications: gray symbols mark agro-pastoral animal production systems. Green symbols: cultivation-oriented livelihoods are indicated by a combination of C_3 cultivation-oriented livelihoods and stock-keeping systems; possible secondary indications: gray symbols mark agro-pastoral animal production systems. Orange symbols, hunting-gathering livelihoods are indicated by the presence of livelihoods oriented toward C_3 or C_4 hunting-gathering; for possible secondary indications, gray symbols mark outlier hunter-gatherers on the southwestern Cape with high terrestrial food reliance and outliers from North African cultivation-oriented clusters. Yellow symbols: aquatic-oriented livelihoods are primarily indicated by aquatic-oriented livelihoods and aquatic-oriented animal production; for possible secondary indications, gray symbols mark herding-fishing-hunting livelihoods.

necessitated interdependence of (agro-)pastoral and hunting-gathering strategies in the Zambezi Basin and whether this prevented an earlier spread of herding in the region (e.g., versus trypanosomiasis for East Africa[106]).

Understanding of how livelihood change feeds into complex subsistence economies requires investigation of material exchange networks (e.g.,[107–110]), underlying social ties[111] and the sharing of resources and social capital between communities, and underlying environmental context, e.g., fire regimes, vegetation change, elevation, climate, and other disturbance feedbacks.[112–117] Such social ties and resulting exchange networks can mediate food security and the stability of socio-ecological systems, particularly during periods of environmental change.[118–121] As network disruptions can cause breakdowns in resilience or restructuring of social organization and interactions,[122–125] this is a key area where modern policies overlooking local context can cause breakdowns in important system interactions and reduce human resilience in the face of environmental change. Therefore, future research should investigate these socio-ecological relationships and evaluate the effects of current policies on livelihood security and resilience.

Exploring livelihood trends in environmental context

Livelihood trends

During and after the termination of the AHP, trends in pastoral-associated livelihoods (blue and red triangles) were linked with specialized animal production systems (Figure S10) and elevation change, reflecting opposing directions between northerly-mid and southerly latitudes (Figure S10: $p < 0.05$). In northern to mid latitudes, $\delta^{13}C$ from human tissues declined through time (i.e., increased association with C_3 plants) alongside an overall shift toward lower elevations (note: specialized pastoral systems also shifted toward lower elevations). Conversely, in southerly latitudes, $\delta^{13}C$ from human tissues increased through time, alongside a shift toward higher elevations (i.e., increased association with C_4/CAM plants and incorporation of pastoralism). During and after the termination of the AHP, trends in C_3 cultivation-oriented livelihoods (green and purple triangles) shifted toward cooler, wetter, and lower elevations (e.g., Nile Valley to Tunisia). The environmental characteristics of C_3-oriented hunting-gathering livelihoods (orange triangles) reflected no significant temporal trends. The isotopic niche of aquatic oriented hunting-gathering livelihoods (yellow triangles) shifted toward environments that are less seasonal and at lower elevations, potentially reflecting complex, changing relationships with pastoralism.

Regional context

Grouped regionally, significant $\delta^{15}N$ trends in northerly and southerly latitudes may reflect a range of drivers (Figure S10). Potential drivers include climate change associated with orbital forcing, i.e., ^{15}N-enriched human tissues in northern latitudes experiencing aridification and ^{15}N-depleted human tissues in southern latitudes experiencing humidification[24] (see also Figure S5; note that these trends are broadly reflected at site level but have complex and variable trends between sites; Table S3). Additional potential drivers include associated regional changes in livelihood practices (Figure S10), which may impact soil nitrogen, e.g., through changes in manuring practices.[36,48] $\delta^{13}C$ temporal trends varied by region: declining $\delta^{13}C$ in the northern to middle latitudes may reflect increased incorporation of cultivation and an associated shift toward lower elevations (Figure S10), potentially in response to regional aridification. Conversely, increasing $\delta^{13}C$ in the southerly latitudes may reflect increased incorporation of pastoralism and an associated shift toward higher elevations (Figure S10), potentially in response to regional humidification. For trends split between the AHP and after the AHP, see Figure S5.

Northeast Africa. In Northeast Africa, human tissues broadly reflected ^{15}N enrichment across the Holocene, regionally and at site level (Figure S10 and Table S3), while $\delta^{13}C$ trends varied among sites and time periods (Table S3). ^{15}N enrichment in Holocene human tissues may reflect Holocene aridification (e.g.,[20,25]) and/or changing agricultural practices, such as increased crop manuring and reliance on animal proteins.

Eastern Africa. Trends varied at site and regional level. During the AHP, $\delta^{15}N$ in human tissues increased and there was no significant trend in $\delta^{13}C$. After the AHP, $\delta^{13}C$ in human tissues decreased despite the continued expansion of the domestic animal niche,[3] and there was no significant trend in $\delta^{15}N$. These varied trends could potentially reflect changes in the composition or extent of East African grassy ecosystems.[3,37,75,126] However, because we observed a close coupling between environmental variables and livelihood strategies (Figure S5 and Table S1), and because pastoral livelihood strategies and specialized pastoralism both shifted toward lower elevations through time (Figure S10), varied trends are more likely to reflect adaptive livelihood responses to climate change, with potential to buffer against environmental change.[127]

Southern Africa. Human tissues became depleted in ^{15}N after the AHP, both at regional scale and at most sites (Figure S5 and Table S3), potentially reflecting increasing southern hemisphere precipitation and/or a shift in regional occupation toward different climatic conditions in the southeast. Despite increasing precipitation in the southern hemisphere, human tissues became enriched in ^{13}C at regional scale. Combined with non-significant $\delta^{13}C$ trends at site level (Table S3), this may reflect complex interactions between vegetation change and increasing pastoral reliance and adaptations.

While ^{13}C trends may potentially reflect anthropogenic changes in the composition and limits of sub-Saharan grassy ecosystems (e.g.,[2,3,20,25,126]), climate and elevation explain large proportions of $\delta^{13}C$ variability (Figure S5), suggesting that livelihood changes may have primarily reflected adaptive responses to climate change rather than land-cover modifications. However, the drivers of human-environment interactions are spatially and temporally complex, requiring further empirical investigation (e.g., Figure S5 and Table S3). Useful future research will include comparisons of our continental-scale approach with regional palaeodiet reconstructions to link continental-scale patterns and trends to quantitative proportional estimates by region (i.e., in p-space; e.g., with SIMMS[62,63]), and contextualization of other priority conservation regions with socio-ecological overlap.[114,128–130]

Conclusion

Understanding how past human societies adapted to environmental change is essential for addressing contemporary sustainability challenges, particularly those related to climate adaptation, food security, and livelihood resilience. Despite Africa's long history of human-environment interactions, there remains a critical gap in understanding how Holocene livelihoods evolved across the continent in response to major climatic shifts, especially the AHP (c. 14,700–5,500 BP). Our study addresses this gap by reconstructing and characterizing isotopic niches and their associated livelihood strategies and demonstrates continent-wide livelihood diversification and its role in shaping resilience to environmental change with implications for understanding and supporting current and future livelihood resilience and food security. Our results reveal that livelihood diversification was a central mechanism for buffering against long-term climatic perturbations, shaping adaptive responses across Africa. We show that while both C_3- and C_4-oriented food-production strategies supported Holocene livelihoods in similar proportions, they followed distinct spatiotemporal trajectories. C_3-oriented cultivation remained spatially restricted (e.g., Nile Valley and Tunisia), whereas C_4-oriented pastoral livelihoods expanded across a broad geographic range, adapted alongside diverse food-producing strategies, and became dominant over the last millennium. The ubiquitous and variable nature of pastoral-associated livelihoods highlights their central role in human resilience to environmental change. Additionally, our study contextualizes the isotopic diversity of hunting-gathering strategies and demonstrates their complex and dynamic relationships with food-production systems. By offering a continental-scale reconstruction of Holocene livelihoods, our study significantly advances the understanding of human-environment interactions in Africa and provides empirical evidence for socio-ecological factors that shaped livelihood sustainability. While previous research has explored localized and regional adaptations to Holocene climatic shifts, a comprehensive analysis of livelihood diversification across diverse socio-ecological contexts has been lacking. Our findings build on prior work by empirically illustrating how pastoral, agricultural, and foraging strategies evolved in response to environmental variability. In doing so, we bridge a key knowledge gap concerning the mechanisms that supported livelihood resilience during and after the AHP). This broader perspective not only enhances our understanding of past adaptive strategies but also provides a comparative framework for informing and assessing contemporary and future challenges, including resilience-building efforts relating to climate adaptation, food security, and sustainable livelihoods.

METHODS

General approach

To identify and characterize Holocene human livelihoods (Figure 3) and associated animal production systems (Figures 4 and 5), we first clustered the isotopic niches of humans and domesticates using the AfriArch database.[61] Second, we identified the livelihood characteristics of each isotopic niche (i.e., cluster) by collating and summarizing the livelihood information published in associated studies (see Figures 2, S1, and S2[60]), and compared the present-day environmental context of each using WorldClim data (Figures 3, 4, and S5). Third, we compared the spatiotemporal patterns (Figure 6) and trends (Figure 5) among the different isotopic niches and their associated livelihoods.

Isotopic niche clustering

We hierarchically clustered isotope signatures (δ^{13}C; δ^{15}N) from human and faunal remains, using the hclust package in R.[103] The Euclidean distance metric was chosen, and the complete linkage clustering method, which splits the dataset based on the maximum value of dissimilarity between clusters (Figure S14). We aimed to include as much information as possible to inform clustering but applied essential pre-clustering filtering and corrections: (1) we averaged δ^{13}C and δ^{15}N values for the same individual, as determined from specimen and Lab IDs; (2) we removed outliers without any clustering neighbors (one human with a C:N ratio of 3.5, initially clustered with samples having a C:N ratio >3.6); (3) we applied Suess corrections to account for shifts in atmospheric CO_2 after the industrial revolution (following Crowley & Godrey [131] we added +0.004‰ for each year that passed from AD 1860 to 1965, plus an additional -+0.02‰ for each year that passed after 1965 (applied to seven modern humans); (4) to facilitate the computation of Euclidean distances in hierarchical clustering and avoid potential issues with negative δ^{13}C values, we uniformly shifted the δ^{13}C data by adding the minimum value plus 1, preserving the relative differences between values.

For the isotopic niches of humans (described herein in terms of their summarized livelihood characteristics, based on published archaeological context[60]), we considered simplified (n = 5) to complex (n = 7) clustering splits. Fewer than five clusters failed to differentiate between pastoral and aquatic-associated clusters; seven clusters allowed meaningful subdivision of the simplified clusters; and more than seven did not provide adequate explanatory benefit. A similar justification was used for the isotopic niches of domestic animals (i.e., summarized animal production systems): fewer than five clusters failed to differentiate between clusters associated with C_4 agro-pastoral and specialized pastoral strategies; six clusters differentiated between stock-keeping strategies; and more than six clusters did not provide adequate explanatory benefit.

Enamel isotopes from domestic fauna were also included with bioapatite-collagen offsets (i.e., δ^{13}C bioapatite −6.8‰ ± 1.4‰[132–134]), providing complementary information for livelihood mapping (Figure 6). Human enamel records were not included here due to lack of δ^{15}N differentiation and potential biases associated with carbohydrates in human foods. Filtering was also applied to improve the accuracy of cluster interpretation for each individual, including: (1) removal of samples that include isotopic averages for more than one individual (three entries from Wadi Halfa, reflecting up to 90 humans); (2) removal of C:N ratios that may reflect poor preservation (47 individuals: Figure S8) (i.e., <2.9, >3.6[135]); and (3) removal of juveniles (<25 years old, as defined in Goldstein et al.[61]) that may fall within a different livelihood category to associated adults, due to breastfeeding/weaning effects (eight individuals: see Figure S7). Note that weaning ages are variable and occur in most contemporary non-industrialized societies around 24–36 months old[136,137]; because the analyzed dataset[61] identifies juveniles as younger than 25 years, we provide supplemental analysis to understand the distribution of juvenile samples across each isotope cluster and to ensure that clusters are not explained by weaning practices (Figure S7).

The isotopic niches of humans and domestic animals were then interpreted in terms of their dominant livelihood and animal production systems, respectively, based on regional to site-based archaeological context.[60] For each niche, isotope values reflected documented ranges associated with relevant diets and environmental conditions (e.g., Dewar et al.[70]) and fit within an existing global-scale characterization of livelihoods and animal production systems.[57,58] Given the close association documented here between African isotopic niches and their dominant livelihood characteristics, we hereafter refer to each isotopic niche by its dominant livelihood strategy, although these entities are not inherently equivalent.

Spatiotemporal patterns

Using the isotopic niches of humans (interpreted in terms of their dominant livelihood characteristics) and the isotopic niches of domestic animals (interpreted in terms of their dominant animal production strategies), we mapped and analyzed the spatiotemporal trajectories of human livelihoods (Figures 5 and 6). This includes the application of methods from niche dynamics to reconstruct and spatially project the climatic niches for each livelihood group based on a modern climate gradient (Figure 6A, i.e., land use or livelihood niches, as applied in Phelps et al.[3]). Further, we describe the environmental context of these patterns, using present-day climate and elevation information (WorldClim v.2[102,138]).

Temporal trends were explored for each isotopic niche, including for humans (summarized livelihoods), domesticates (animal production systems), and regions, using ordinary least-squares regression. Some trends reflect change across the Holocene, while others were split into two intervals to explore tendencies during and after the AHP. The number of samples through time was compared with livelihood composition to ensure that sampling bias does not explain livelihood trends (Figure S15).

RESOURCE AVAILABILITY

Lead contact

The lead contact for this paper is Leanne N. Phelps (leannenphelps@gmail.com).

Materials availability

This study did not generate new unique materials.

Data and code availability

All original R code used for analysis in this study has been deposited at GitHub at this link, and is publicly available as of the date of publication. The data produced by this study (for the livelihood summarization and associated clusters) are publicly available as of the date of publication at https://doi.org/10.5061/dryad.6djh9w1b0.[60] This study analyzes existing publicly available data published by Goldstein et al.[61]: http://doi.org/10.5334/joad.94.

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AUTHOR CONTRIBUTIONS

Manuscript conception, design, and first draft, L.N.P.; manuscript discussion and development, K.D., D.S.D., J.C.C., S.M., and C.M.; second manuscript draft, L.N.P.; additional feedback and development, K.D., D.S.D., J.C.C., S. M., C.M., and C.E.R.L.; figures, L.N.P.

DECLARATION OF INTERESTS

The authors have no competing interests to declare.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During final revisions of this work, ChatGPT was used to generate revision ideas in response to editorial comments and to ensure that the revised text met the instructions asked. After using this tool/service, the content was selectively chosen, reviewed, and extensively modified as appropriate. The authors take full responsibility for the content of the publication.

SUPPLEMENTAL INFORMATION

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