


Opinion

Rethinking the ecological drivers of
hominin evolution

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A central goal of paleoanthropology is understanding the role of ecological change in hominin evolution. Over the past several decades researchers have expanded the hominin fossil record and assembled detailed late Cenozoic paleoclimatic, paleoenvironmental, and paleoecological archives. However, effective use of these data is precluded by the limitations of pattern-matching strategies for inferring causal relationships between ecological and evolutionary change. We examine several obstacles that have hindered progress, and highlight recent research that is addressing them by (i) confronting an incomplete fossil record, (ii) contending with datasets spanning varied spatiotemporal scales, and (iii) using theoretical frameworks to build stronger inferences. Expanding on this work promises to transform challenges into opportunities and set the stage for a new phase of paleoanthropological research.

Challenges and progress in hominin paleoecology

Hominin paleoecology seeks to understand the relationships between the evolutionary history of fossil hominins and the ecosystems in which they lived. Key questions include: (i) was global-scale climate change a major driving force in hominin diversification? (ii) Did paleoenvironmental dynamics influence hominin morphological and behavioral adaptations? (iii) Were changes in community structure and biotic interactions important in shaping hominin evolution and extinction? Attempts to answer these questions have fueled the recovery of paleoclimatic, paleoenvironmental, and paleoecological records [1–5], and the development of sophisticated analytical tools [6–8], but this progress has not always led to a deeper understanding of hominin evolution [9–12]. This stems from the limitations of research strategies that focus on linking temporal patterns of ecological change with milestones in hominin evolution – such as speciation and extinction events or shifts in hominin behavior – and inferring causal relationships between the two [9]. How can hominin paleoecology move beyond this pattern-matching paradigm to generate enduring insights about the influence of ecological change on hominin evolution?

Capitalizing on the growing body of empirical data requires that hominin paleoecology rethinks its strategy for formulating research questions and how they are answered. We examine several theoretical and epistemological challenges that have long hindered the development of robust evolutionary insights, and highlight how recent research is addressing them. This work (i) confronts the limitations of an incomplete fossil record, (ii) contends with proxy records that span a considerable range of **spatiotemporal scales** (see [Glossary](#)), and (iii) uses theoretical frameworks that link ecology and evolution to build stronger inferences ([Figure 1](#)). Our goal is to highlight promising new research directions that move beyond inferences based on ecological and evolutionary pattern-matching to a deeper understanding of causality in hominin evolutionary history.

Highlights

Research aiming to understand the role of ecological change in hominin evolution has fueled the generation of paleoclimatic and paleoenvironmental records across Africa.

Limitations of conventional methods for inferring ecology–evolution relationships mean that more data have not always led to a deeper understanding of hominin evolution.

We outline several challenges that have hindered progress, and highlight how recent research is addressing them.

This research is confronting the limitations of the fossil record, contending with proxy records spanning a range of spatiotemporal scales, and providing a stronger inferential approach to hypothesis testing.

Addressing the obstacles that have hindered progress will enable a more robust understanding of the relationships between ecological change and hominin evolution.

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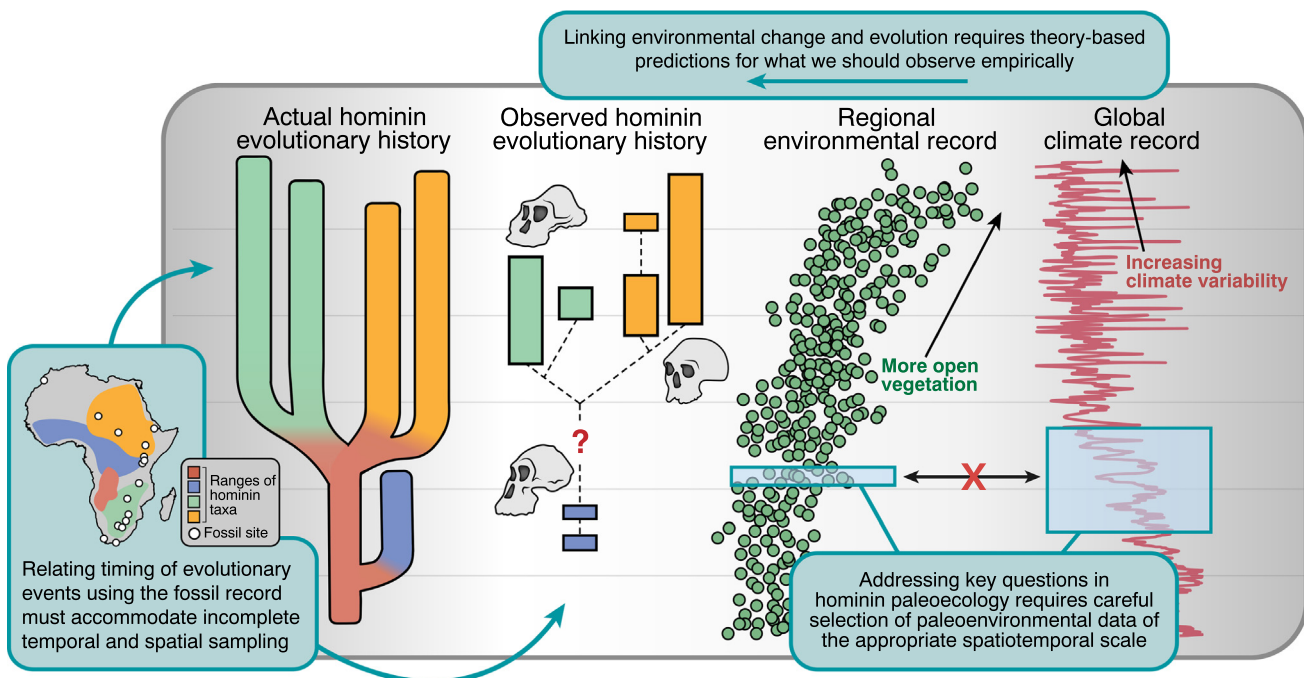
Confronting an incomplete fossil record

To begin to understand why hominin paleoecology is not providing more informative evolutionary insights, a frank appraisal of the limitations of the hominin fossil record, and their implications for the types of questions we can answer, is warranted. These limitations stem from a hominin fossil record derived from the few places where (i) hominins were present, (ii) their remains were buried in a **depositional environment** conducive to preservation, (iii) tectonic forces and erosion are currently exposing these remains such that they are at, or near, the surface, and (iv) researchers have conducted fieldwork leading to their recovery. The locations and geological time-intervals meeting these criteria are only a subset of where and when hominin taxa actually occurred, resulting in an incomplete fossil record characterized by spatiotemporal gaps [13,14] (Figure 2). It is estimated that the hominin fossil record samples less than 1–2% of Africa's landmass [15], limiting us to a few small windows into the spatial extent of hominin evolution. Moreover, temporal sampling is patchy within these small spatial windows, making it difficult to identify when and where key evolutionary events took place [16] (Figure 2). These impediments are compounded by the rarity of hominin fossils relative to many other mammalian taxa [17].

A consequence of the spatially and temporally limited hominin fossil record is that many evolutionary changes of interest are overprinted by sampling artifacts. Analysis of the eastern African fossil record shows that the number of hominin species observed at any time is largely determined by the combination of fossil collection effort and the amount of sedimentary rock available for sampling [14], implying that the existing picture of hominin evolution and **taxic diversity** is far from complete [15]. Likewise, the incompleteness of the record from southern Africa is exemplified by the recent discoveries of two new hominin species (*Australopithecus sediba* and *Homo naledi*)

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Figure 1. Linking paleoecological change with hominin evolution. Recent advances allow hominin paleoecologists to address challenges in understanding how ecological change influenced hominin evolution. These challenges include the need to account for gaps in the hominin fossil record, align the spatiotemporal scales of the empirical data and the research question, and build stronger inferences using theoretical frameworks that generate testable predictions.

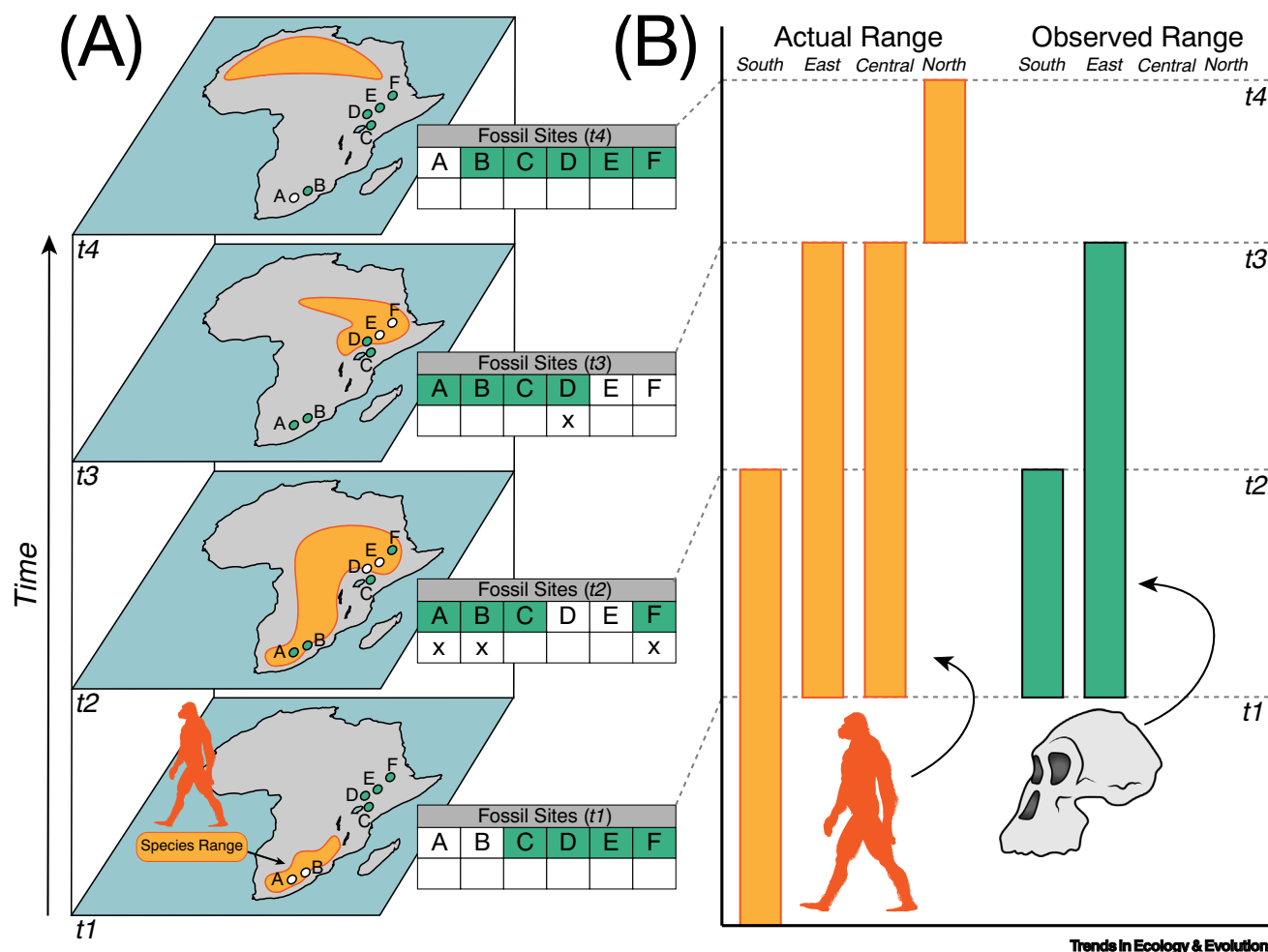


Figure 2. Spatiotemporal limitations of the hominin fossil record. (A) A hypothetical hominin's geographic range through time is represented in yellow. Fossil sites with sediments dating to a given time-period are in green, although only a subset of these sites overlap with the hominin's range and preserve hominin fossils (indicated with an x); sites lacking a sedimentary record during a time-bin are in white. (B) Spatiotemporal gaps in the fossil record mean that the fossil evidence (observed range, green bars) documents a subset of the hominin's actual distribution through space and time (actual range, orange bars).

in a region that has been well studied for decades [18,19]. In general, incomplete sampling means that the observed temporal and geographic ranges of fossil hominins and their archaeological traces will tend to be underestimated (e.g., observed **first appearances** are too young and **last appearances** are too old; Figure 2). This is important for understanding key milestones in hominin evolution – such as technological innovations, changes in morphology, or speciation and extinction events – which are subject to ongoing revision as we continue to recover new fossil and archaeological evidence.

An incomplete fossil record prone to sampling effects limits what we can know about hominin evolution, but conventional strategies in hominin paleoecology have not always acknowledged this. Consider, for example, the origin of the genus *Homo*. Decades of research has focused on whether environmental change, such as grassland expansion or environmental instability, led to the divergence of *Homo* from its precursors [20]. Addressing this requires, among other

things, knowing when and where *Homo* emerged. This leads to two problems. The first is that, because of the poorly sampled fossil record, the current understanding of when and where [21] will almost certainly continue to be revised. The second and more serious problem is the possibility that *Homo* emerged in an area outside the regions that provide most of the fossil evidence [22]. This would mean that the oldest fossils attributed to *Homo* are unlikely to document the emergence of the genus, but instead record its subsequent dispersal into a region that fulfills the four criteria set out earlier [23]. Attempts to explain other milestones in hominin evolution, especially those that occurred in poorly sampled time-periods, are confounded by similar sampling problems.

There are productive avenues for future research if we work within these constraints by asking questions and using analytical frameworks that acknowledge sampling limitations. Researchers are beginning to do so by applying quantitative methods developed in ecology and paleobiology [24,25] to more effectively confront the reality of an incomplete fossil record. The importance of adapting research approaches to the limitations of the hominin record has been noted before [16], but there has only been a concerted effort to do so in the past several years [26–29]. This includes quantifying the chronological uncertainty about the first appearances (origination/emigration) and last appearances (extinction/emigration) of hominin taxa within **depositional basins** [26,28], as well as estimating hominin origination and extinction dates [27] and the timing of developments in stone-tool technology [29]. Results of these efforts can be sobering [the mean uncertainty around origination and extinction is potentially ~0.5 million years (Ma) (S.J. Maxwell, PhD thesis, University College London, 2018)], demonstrating substantial uncertainty about the observed stratigraphic ranges of hominin taxa, confirming that the hominin fossil evidence often grossly underestimates true temporal ranges (Figure 2) and reinforcing the difficulties of trying to link such evidence to ecological change.

In addition to providing a useful reality check, these quantitative tools have helped paleoanthropologists to assess evolutionary relationships between hominin taxa [27,30] and to explore ways that patterns of hominin diversity might be related to ecological change [26]. These methods also provide untapped potential to estimate the ages and stratigraphic placement of major faunal **turnover** events [31], or to evaluate phylogenies and taxonomic attributions that are often the basis of paleoecological analysis [32,33]. By continuing to draw from, and ideally contribute to, methodological developments that help to contend with an incomplete fossil record – work that has largely been the domain of paleobiologists – hominin paleoecologists will gain a deeper understanding of the uncertainties surrounding the empirical evidence. This will help to direct our efforts towards tractable research questions, temper interpretations to reflect the realities of the fossil record, and more effectively link paleoecological and evolutionary change.

Aligning the scales of the questions and the data

A second fundamental challenge involves acknowledging the scales of the research questions and the empirical evidence. The paleoecological data bearing on hominin evolution span a massive range of spatial, temporal, and taxonomic scales (Figure 3). Paying attention to these scales is crucial because ecological patterns and processes vary across them [34,35]. For example, if researchers followed a herd of zebras across a grassy floodplain, they would notice that the herd avoids places frequented by lions. However, if they examined the spatial distribution of zebra across a $1^\circ \times 1^\circ$ grid superimposed on Africa, they would instead observe that zebra occur in many of the same places as lions, with habitat being an important predictor of zebra spatial distributions. Changing the scale of observation alters the apparent spatial relationships between zebras and lions (segregated versus aggregated) and the proximate variables influencing zebra spatial distributions (predators versus habitats). There is no universally 'correct' scale of

Glossary

Biomarkers: molecular fossils (e.g., organic compounds) that are preserved in soils and sedimentary records, and which are indicative of past environments, climates, and fire regimes.

Depositional basin: in geology, a region of the Earth's surface where there is net accumulation of sedimentary deposits over time that may also preserve a fossil record.

Depositional environment: in geology, the physical environment in which sedimentary rocks are formed (e.g., floodplains, rivers, lakes, oceans) that are identified on the basis of lithofacies characteristics (e.g., sediment type and bedding structures).

First/last appearance: respectively, the oldest and youngest appearance of a taxon in the fossil record, which together define the observed temporal range of the taxon. These dates are frequently revised with new fossil discoveries.

Generative model: computer simulations illustrating the macroscale patterns that emerge through the microscale interactions of individual system components over time.

Mesowear: the macroscopic wear patterns on an animal's teeth that result from processing foods with different mechanical properties.

Microwear: the microscopic wear patterns on an animal's teeth that result from processing foods with different mechanical properties.

Naturalistic: observations based on natural systems. In **taphonomy**, for example, this refers to studies in which taphonomic processes (e.g., bone consumption by carnivores) are observed in the absence of experimental manipulation.

Orbital cycles: also known as Milankovitch cycles, these are cyclical variations in Earth's orbit (eccentricity, precession, obliquity) that drive climate change over geological timescales.

Soil carbonate: CaCO_3 precipitated during soil formation, usually in seasonally dry environments. They record carbon and oxygen isotope ratios that reflect the dominant vegetation or soil water system dynamics (e.g., evaporation), respectively.

Spatiotemporal scale: the spatial and temporal scales over which a process or phenomenon occurs. In hominin paleoecology, spatial extents often

observation, but to address questions linking ecology and evolution, the scales of the processes of interest must align with the scales of the available data [35,36].

Many questions in hominin paleoecology involve processes that play out over large spatiotemporal scales (Figure 3), but accepted research strategies have not always ensured that the scales of the datasets used to address them are appropriate. For example, it has been routine to begin with questions – such as those pertaining to the emergence of a species or an archaeological transition – that require data collected across large spatial scales, and then attempt to answer them with datasets that represent smaller spatial scales. Returning to the zebra example, we cannot reasonably expect to understand their habitat associations across Africa by studying one herd on a grassy floodplain. This is an inappropriate scale of observation given the objective, and the interpretation would change if the focus were a different herd of zebras in another type of habitat. Scale misalignments of this kind are why researchers offer contradictory interpretations about the ecological drivers of hominin evolution when they consult different paleoecological records that are subject to different basin-scale climatic, environmental, and tectonic histories (*cf* conflicting interpretations in [37,38]). Individual records are the foundation of our knowledge – and their value is amplified when multiple datasets can be combined to study phenomena across a variety of scales – but, on their own, they are not necessarily suited to addressing the larger-scale questions.

Different challenges are posed by the temporal scale of the data. For example, habitat reconstructions of hominin fossil localities are commonly presented as static descriptions of the local-scale environment in which a hominin lived (reviewed in [10,39]). However, the proxies that form the basis of those reconstructions often record the environment over timescales of thousands to hundreds of thousands of years [39]. This **time-averaging** leads to mixing of different environmental signals, thus masking variability that may be relevant to the question at hand [36,39]. When dealing with biotic proxies (e.g., flora and fauna), time-averaging is equivalent to sampling across larger spatial scales because more time in a sediment package results in the recovery of more species from outside the immediate study area [40–42]. If the environment is changing, and species disperse into an area as they track their preferred habitat, then the effective spatial scale of the data further increases [36,39]. Thus, as paleoenvironmental data are progressively time-averaged, the spatial scale shifts from local – which is usually the interpretive focus – to regional and beyond. It follows that, except when time-averaging is negligible (e.g., [28,43]), the reconstruction of a hominin locality as, for example, a wooded grassland does not necessarily imply that the hominins found there ever lived in this setting or that such a place even existed. This situation could occur if the fossil assemblage was a time-averaged mix sampling a floodplain grassland adjacent to a riparian woodland, with an ecotonal boundary that shifted across the locality over time.

Recent progress is helping hominin paleoecologists contend with these scale-related challenges. Building on work in paleobiology concerned with the consequences of time-averaging (e.g., [41,42,44]), there is a growing appreciation of the spatiotemporal scales of the data used by hominin paleoecologists [40,45–47]. For example, stable carbon isotopes of fossil herbivore teeth and **soil carbonates** often provide distinct environmental signals, even when they are from the same localities, because the two proxies sample the environment at differing spatiotemporal scales (e.g., soil carbonates provide a local, time-averaged signal, whereas herbivore teeth provide a landscape-scale, less time-averaged signal [45]). Similarly, it has also become clear that discrepancies between the different paleodietary proxies used to understand hominin ecology and paleoenvironments (e.g., stable isotopes, **mesowear**, **microwear**, and morphology) are a consequence of those proxies recording diet over different timescales [46]. This means that synthesizing or comparing observations from different

range from local to continental, and temporal extents from several years to millions of years.

Taphonomy: the study of the processes involved in the formation of the fossil record (e.g., death, decay, scavenging, burial, mineralization), and how these processes affect the information preserved in fossil samples of past life.

Taxic diversity: the number of species in a biotic community; in the context of the hominin clade, this refers to evidence that it included more than one species at any given time.

Time-averaging: the outcome of geological and taphonomic processes that control how much time is represented in a fossil assemblage (taphonomic time-averaging), or analytical decisions concerning how to aggregate fossil samples from different stratigraphic horizons or localities (analytical time-averaging).

Turnover: a change in species composition through time as a result of speciation, extinction, and dispersal.

Turnover-pulse hypothesis: a model of macroevolutionary change developed by Elisabeth S. Vrba by which climate-driven changes in habitats leads to a synchronous peak in turnover (extinction, speciation, and dispersal) across multiple lineages. Vrba applied this model to the African record, proposing that global cooling between 2.8 and 2.5 Ma led to a major turnover pulse that included the first appearance of *Homo* and *Paranthropus* [51,68].

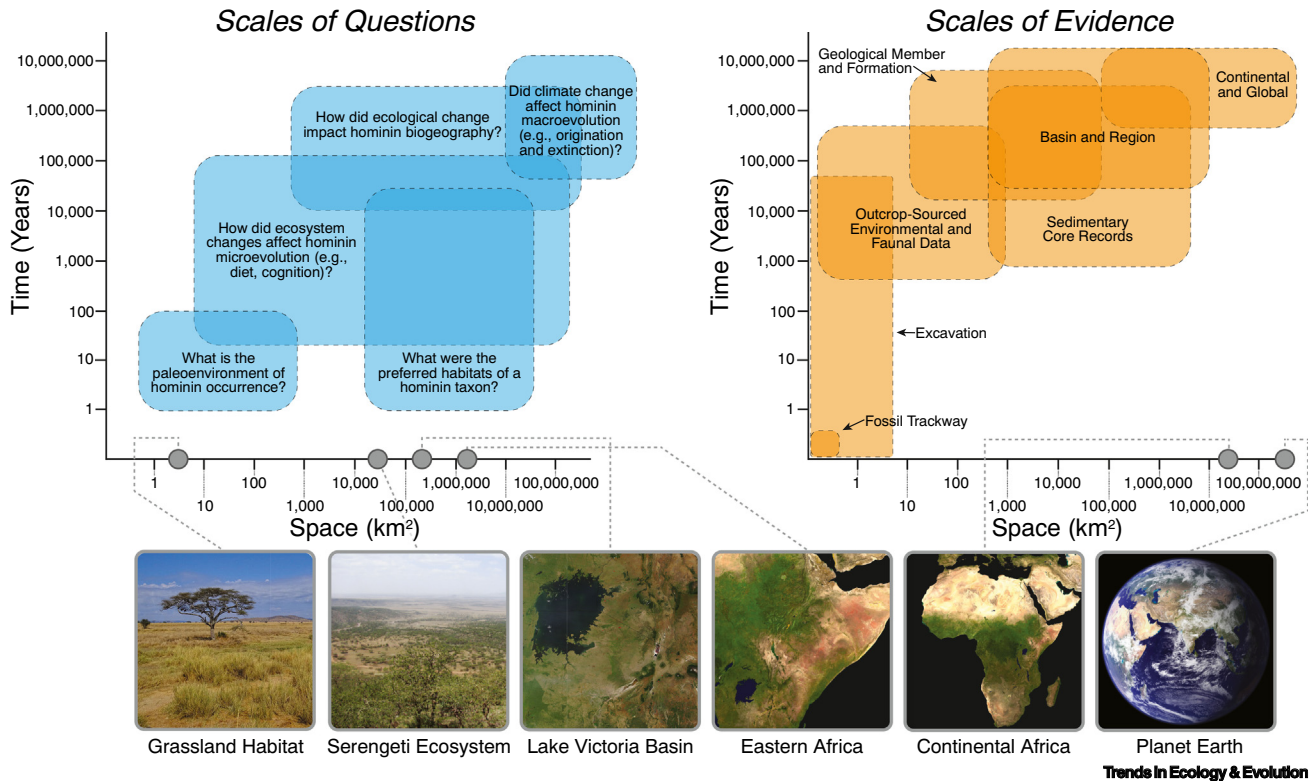


Figure 3. Aligning spatiotemporal scales. The research questions of interest, and the data used to address them, span a considerable range of spatiotemporal scales. Problematic 'scale-jumping' occurs, for example, when inferences based on finer resolution evidence (e.g., one grassland habitat that existed for hundreds of years) are assumed to represent a much larger area (e.g., eastern Africa) or a longer time-period (e.g., 10^3 years to 10^5 years).

proxies, or even the same proxies that are differentially time-averaged, is a more complicated undertaking than it might first appear.

Further developments are allowing researchers to address these complications. **Generative models** are computer simulations that illustrate the macroscale patterns that emerge through the microscale interactions of individual system components over time (e.g., between hominins, food resources, and environments), and they are being used to bridge scales between the processes of interest and the data used to study them. For example, this approach has been used to contend with the varying timescales of paleodietary proxies [46] by simulating the dietary signals provided by the dental microwear (recording the last few weeks of life) and stable isotopes of tooth enamel [averaged over the year(s) in which a tooth develops] in time-averaged fossil records from different environments [48]. These simulations can indicate patterns in the two proxies that reflect different environments, facilitating their interpretation. Ecologists are also embracing these approaches to bridge scales [49]; recent work, for example, uses simulations to explore how the processes that influence the geographic ranges of individual populations and species scale-up to create continental-scale biodiversity patterns [50]. There is potential to leverage generative modeling to address many situations where the scales of the processes of interest differ from the scales of the data at hand (e.g., studying the effects of **orbital cycles** on ecosystems using datasets that are time-averaged over multiple cycles).

As we continue to learn more about the scales of the proxy records, and how to contend analytically with their implications, hominin paleoecologists will be able to more effectively align the scales of the

data with the scales of the questions. The more scale-aligned paleoecological studies there are, the greater the potential for comparative research to reveal common patterns based on multiple fossil sites and proxies that indicate links between ecological change and hominin evolution.

Building stronger inferences

A final challenge in hominin paleoecology relates to how we infer causal relationships between ecological and evolutionary change. Conventional strategies often begin with reconstructing paleoecological change through time at a given location (e.g., site, depositional basin, or region) using one or more forms of proxy evidence. These proxies are derived from the paleontological and geological record, and include fossil faunas and plant microfossils (pollen and phytoliths), as well as the geochemistry of fossil teeth, **biomarkers**, and soil carbonates. Researchers then search for matches between the temporal patterns in the paleoecological data and the timing of evolutionary milestones in hominin evolution, propose causal links between them, and offer suppositions about how ecological change influenced hominin evolution.

This pattern-matching formula does not lend itself to robust inference. With some notable exceptions (e.g., [51,52]), inferred relationships between ecology and evolution have been made without first outlining why a relationship should exist, or setting out expectations about what we should observe empirically. In the absence of such process-based thinking, there has been a tendency to formulate explanations after interrogating the empirical records. When an incomplete paleoanthropological record (Figure 2) is coupled with imprecise and qualitative paleoecological observations (e.g., fossil assemblages indicate a wooded grassland), any number of interpretations can explain the observed associations between ecological and evolutionary change. Because such explanations originate from patterns in the data, by definition they fit and explain those data, making *post hoc* hypotheses difficult, if not impossible, to falsify. A consequence is that it is easier to accumulate new hypotheses than to reject them [53], and there is now a plethora of environmental hypotheses claiming to account for important milestones in hominin evolution [54–56]. The abundance of hypothesized drivers of hominin evolution (e.g., grassland expansion, aridity, environmental instability; Box 1) means that the conventional pattern-matching strategy has almost always resulted in observations that speak to one or more of these drivers. Perhaps the implicit hope is that if this pattern-matching exercise is repeated often enough, a clear front-runner will emerge, but this has not happened.

The solution is to place greater emphasis on theory-driven prediction, in which theoretical frameworks linking ecology and evolution are used to set up predictions that are tested with the data (e.g., [9,48,57]). Theory – by which we mean an explanatory framework for how a natural system works [58] – can come from many sources: by reasoning from first principles [59,60], by applying the comparative method using observations from contemporary non-human primates and human populations [61–63], or by experimentation and **naturalistic** observations [64,65]. Familiar examples of theoretical frameworks linking ecology and evolution include the models provided by behavioral ecology, which archaeologists use to generate predictions about the role of ecological change in driving human diet, technology, or landscape use [66,67]. In the macroevolutionary realm, Vrba's **turnover-pulse hypothesis** [51,68] was constructed with broad theoretical underpinnings that outlined how climate change could drive speciation, extinction, and dispersal, providing clear predictions that could be evaluated with fossil evidence [69–71].

Despite the acknowledged importance of theory-driven prediction in anthropology and ecology [58,72], there have been barriers to operating within this framework. These include difficulties involved in moving from theory to empirical prediction, especially when dealing with time-averaged records that reflect the complex interactions and feedbacks between hominins and the ecosystems in

Box 1. Environmental hypotheses of hominin evolution

Numerous environmental mechanisms are hypothesized as drivers of hominin speciation and extinction, morphological change, behavioral evolution, and dispersals (reviewed in [54,55]). Many are based on observed temporal associations between environmental changes and hominin evolution.

Grassland expansion

The savanna hypothesis proposes that the expansion of grassland ecosystems was fundamental to hominin evolution and adaptation, including the emergence of the hominin clade (reviewed in [54]). Hypotheses linking aridity and/or global cooling to hominin evolution, including Vrba's [51] **turnover-pulse hypothesis**, suggest that the expansion of grasslands was a consequence of these climatic changes and facilitated the emergence of *Homo* and *Paranthropus* (also [91]).

Eastern African coastal forests

The coastal refuge hypothesis proposes that the belt of forests along the coastline of eastern Africa served as a refugium for hominin populations during harsh climate phases, and that biogeographic isolation within these refugia led to allopatric speciation [22].

Environmental instability

Instead of emphasizing adaptation to a particular environment, the variability selection hypothesis proposes that key milestones in hominin evolution were shaped by environmental instability through time and space [92].

Extreme climate variability

Closely related to the variability selection hypothesis, the pulsed climate variability hypothesis emphasizes the role of extreme wet–dry cycles recorded in the eastern Africa record as a driver of hominin speciation and dispersal [93].

Recurrent humid episodes

Abrupt climatic shifts leading to humid conditions in southern Africa are hypothesized drivers of behavioral innovations associated with early *Homo sapiens*, where increased humidity promoted favorable coastal refugia, higher population sizes, and greater inter- and intra-group networking [94].

which they lived. For example, given a theoretically informed model of how a process works, such as hominin foraging behavior in relation to particular habitats, what are the expected empirical patterns in fossil samples from different environments? Generative modeling is one way to address this challenge. This approach can facilitate the formulation of testable predictions concerning expected empirical observations under different scenarios, including those that incorporate the crucial temporal depth that present-day field observations and laboratory experiments cannot capture (e.g., [9,48,73]) (Figure 4). Recent examples have used simulations to make predictions about the environmental conditions under which hominin adaptations are likely to arise [74,75]. Others have used generative modeling to predict how dietary change (e.g., tuber consumption) leads to different hominin ranging patterns [76], how behavioral shifts translate to life history evolution over geological timescales [77], and how environmental change can drive hominin dispersal [78–81] and extinction [82]. The value of these simulations is that, by generating testable predictions, they support the implementation of a more robust, theory-driven inferential framework (Figure 4).

What should be done when there is no existing theory linking ecology to the evolutionary changes that hominin paleoecologists want to explain? The lack of well-established theory in hominin paleoecology is an important challenge, and highlights the need for theory development (see Outstanding questions). For example, researchers are interested in determining whether and how climate change influenced the evolution of hominin brain size [83], but the theoretical links between the two are poorly developed. Establishing those links means first understanding what drives brain size variation within and among living species [84], which then sets the stage for formulating predictions that can be evaluated with fossil data. More broadly, there is abundant potential to examine hominin paleoecology through the theoretical frameworks of allied disciplines, such as community ecology (e.g., ecological niche theory [85,86]), macroecology (e.g., biodiversity theory

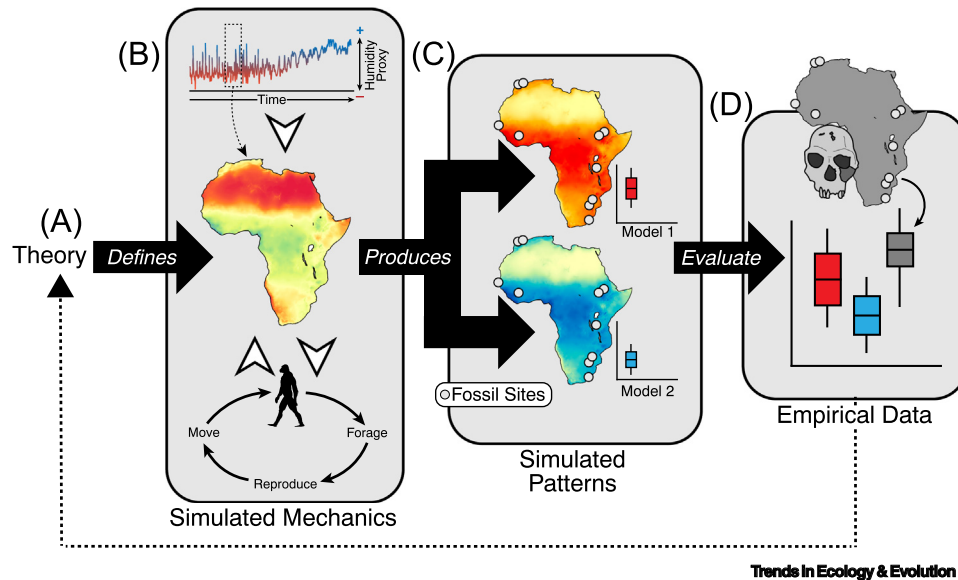


Figure 4. Generative modeling for stronger inferences. Theory (e.g., optimal foraging theory; panel A) informs a generative model simulating the mechanics of a hypothetical hominin ecosystem (B). This hypothetical model simulates hominin diet in relation to an African landscape informed by a humidity time-series record, with hominins interacting with the landscape through time. Models are aimed at 'growing' alternative simulated patterns (C). In this example, the patterns are paleodietary signatures that emerge across African fossil sites under different environmental configurations (e.g., arid versus humid; model 1 versus model 2). Configurations that produce outcomes similar to the empirically observed data (the grey boxplot in panel D) provide a candidate explanation that can be used to make additional predictions and further refine theoretical understanding (broken line).

[87,88]), or paleobiology (e.g., Red Queen and Court Jester [89,90]). Incorporating a stronger theoretical framework into the agenda of hominin paleoecology will allow researchers to reverse the typical direction of inference (i.e., from data to hypothesis) by generating theoretically informed predictions that are tested with the data, and then determining if a hypothesis should be modified or rejected. This would lead to a healthier balance between inferring evolutionary narratives from the data and testing process-based hypotheses using those data.

Concluding remarks

Over the past several decades researchers have focused their efforts on reconstructing late Cenozoic paleoclimatic and paleoenvironmental changes and fleshing out aspects of hominin evolution that demand explanation. This wealth of data, which is the outcome of efforts by numerous international teams, deserves a research agenda that extends beyond the pattern-matching paradigm that has dominated hominin paleoecology. An expanding body of research is adopting strategies to (i) adapt our analyses to cope with an incomplete fossil record characterized by spatiotemporal gaps, (ii) analyze variably time-averaged datasets spanning a diversity of spatiotemporal scales, (iii) approach our questions with theoretical frameworks that link ecology and evolution to generate testable predictions (Figure 1). Collectively, this work provides strategies to direct research efforts towards tractable questions and more effectively utilize the growing body of empirical evidence. If we continue to build on this research (see Outstanding questions), hominin paleoecologists will transform obstacles into opportunities and generate a more robust understanding of the role of ecological change in hominin evolution.

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Outstanding questions

What is the uncertainty surrounding the chronology and spatial distribution of the evolutionary milestones in hominin evolution? Previous work has focused on the temporal ranges of eastern African hominins, but other regions and milestones (e.g., technological innovations, dispersal events) require attention.

What spatiotemporal scales do our proxies reflect? A better understanding of the different scales of the data will allow the comparison and synthesis of proxies that sample variable amounts of space and time.

How can we more effectively synthesize individual paleoenvironmental and paleoclimatic records derived from different proxies? Integrating numerous individual records will be essential for understanding the regional-to-continental changes that are relevant to large-scale research questions.

How can we develop a more robust body of theory to understand hominin evolution, and how can we better translate theory to empirical prediction? This is crucial for a stronger inferential framework, and encourages hominin paleoecologists to draw from theoretical underpinnings of closely allied disciplines (e.g., macroecology, community ecology, paleobiology).

How have biotic interactions such as predation or competition shaped hominin evolution? There has been a historical emphasis on studying the climatic drivers of hominin evolution, and the role of biotic interactions demands more attention.

evidence that is allowing a new phase of research in understanding hominin evolution. Brian Coddling, Kate Fish, Nick Hebdon, Kristen Hawkes, Randy Irmis, Kaedan O'Brien, Jim O'Connell, Andrea Stephens, and two anonymous referees provided helpful feedback on previous drafts. J.T.F. and B.D. were supported by the National Science Foundation (award 1826666).

Declaration of interests

The authors have no interests to declare.

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