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Paleoecology: The Functional Uniqueness of Ancient Megafauna

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https://doi.org/10.1016/j.cub.2019.11.017

Reconstructing prehistoric animal communities is important for understanding the emergence of modern ecosystems and the environmental context of human evolution. A new study of African fossils spanning seven million years shows that ancient large-herbivore assemblages were functionally distinct from those that exist today.

Large herbivores and carnivores occupy a special place in human imagination. They have always featured in our art, from stone-age European paintings [1] to African folktales [2] and North American children's books [3]. Our fascination with such megafauna must stem in part from the fact that they have been important throughout human evolutionary history — as prey to be hunted, as predators to be avoided, and as potent engineers of the environment. Today, there are fewer large mammals in ever-fewer places. They are star attractions at zoos, and they are stalked by tourists in places that have been set aside for them in a world dominated by people. But this is drastically different from the world in which early hominins evolved — a world shaped by enormous carnivores, ungulates, and proboscideans. Understanding the history of humanity, therefore, requires understanding the history of megafauna. A new study by Tyler Faith, John Rowan, and Andrew Du [4] shows that early hominins lived in African environments with megafaunal communities that were unlike any existing today.

Stated in such superficial terms, this finding may not sound surprising. Faith and colleagues [4] analyzed data from 101 fossil large-herbivore assemblages in eastern Africa that reach back into the Miocene, 7 million years ago, which is considerably longer than most large-mammal species persist on the planet [5]. Even on much shorter timescales, there has been dramatic change in mammal communities. Many species and lineages of large mammals were extinguished during the Pleistocene. There are no modern analogs of animals such as the elephant-sized South American giant ground sloths, the hippo-sized Australian marsupial *Diprotodon*, or the clawed, knuckle-walking chalicotheres — a once-widespread group of bizarre-looking herbivores related to horses and rhinoceroses. That ancient mammal assemblages were 'distinct' from modern ones goes without saying.

But Faith and colleagues [4] were asking a different question: to what extent were fossil communities functionally

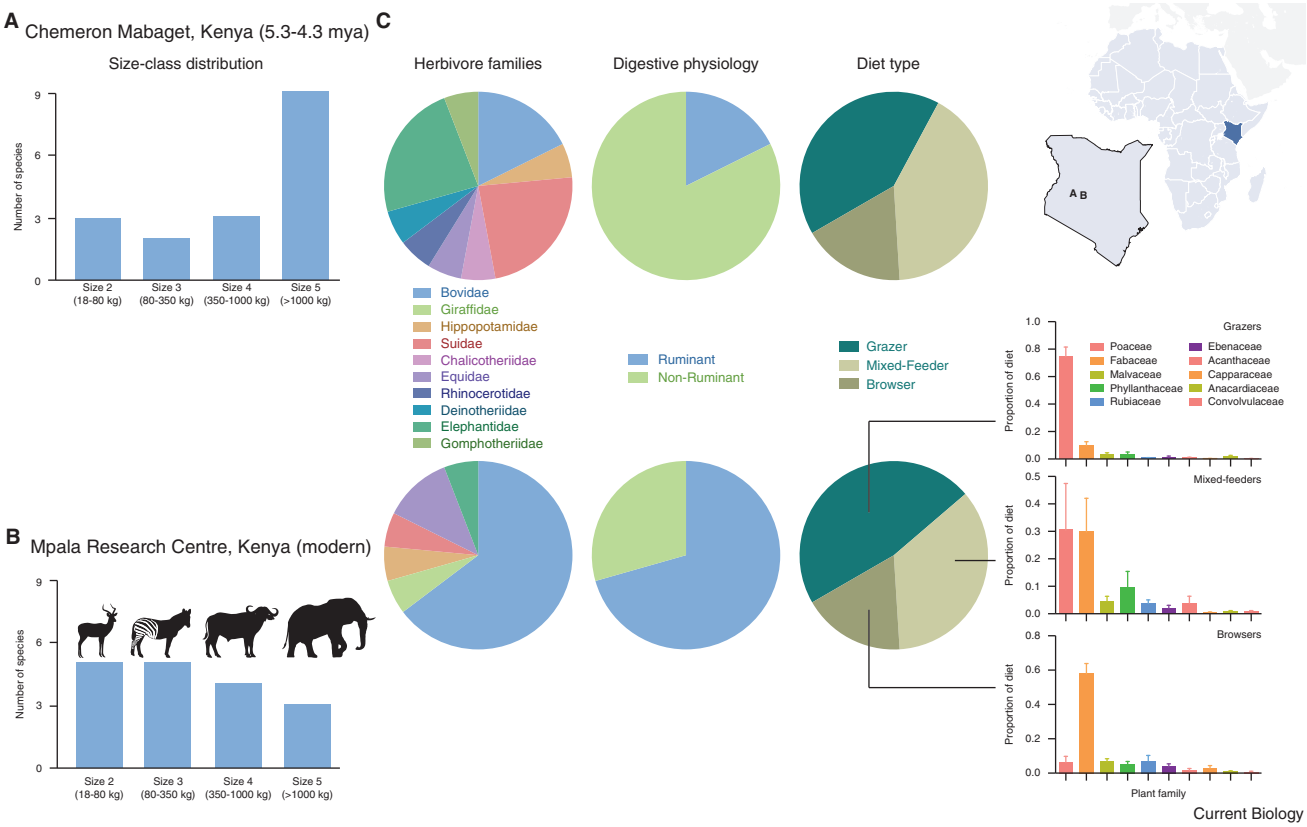

Figure 1. Two large-herbivore communities, one ancient and one modern, in central Kenya.
(A) Data from the study by Faith and colleagues [4] on a Pliocene assemblage of 17 large-herbivore species from the Chemeron Formation, showing the distribution of body sizes and the representation of herbivore families, digestive physiologies, and diet types. (B) Corresponding data for a modern assemblage of 17 species (16 wild large herbivores larger than 18 kg, plus cattle) at the Mpala Research Centre, ~100 km away from the fossil site. (C) For each of the diet types in the modern assemblage, the proportional representation of the top-10 dietary plant families is shown at right, based on data from [20]. These fine-grained dietary data (mean ± s.e. across species in each diet type) are based on fecal DNA metabarcoding, one approach that might facilitate mechanistic investigation into the linkages between the functional traits, diets, and ecological effects of large herbivores. All plots use the taxonomic and trait assignments of Faith and colleagues [4].

analogous to modern ones, and when did they become so? To assess functional analogy, they compared the 101 fossil assemblages with 204 modern ones in terms of three functional traits. The first trait, body size, was broken down into four bins, from mesoherbivores weighing 18–80 kg to megaherbivores >1000 kg. The second trait, digestive physiology, refers to the distinction between ruminants (herbivores that ferment food in the foregut, such as antelopes, buffaloes, and giraffes) and non-ruminants (hindgut-fermenting herbivores such as elephants, rhinos, horses, and pigs). The third trait, dietary strategy, encompassed three groups: grazers that predominantly eat grasses (C_4 plants), browsers that predominantly eat woody plants and forbs (C_3 plants), and mixed-feeders that eat substantial amounts of both C_3 and C_4 plants. Thus, the three traits comprise a total of nine categories. These attributes are linked with differences in the effects that large herbivores have on ecosystems. Large-bodied species and non-ruminants consume greater quantities of plant biomass, whereas small-bodied species and ruminants generally forage more daintily on the most nutritious plant parts [6]. Browsers open up habitats by killing trees; grazers promote tree growth by consuming the grasses that compete with trees and fuel fires [7].

Faith and colleagues [4] found that from 7 million to 700,000 years ago, all but a handful of communities in eastern Africa were functionally non-analog — almost no assemblages over this span of 6.3 million years fell within the range of modern variation for all of the trait categories. Compared with modern communities, fossil assemblages included more species of megaherbivore (>1000 kg), fewer species of mesoherbivore (18–80 kg), and more species of non-ruminant (Figure 1). The temporal trends in dietary strategy were nuanced and more likely to fall within the range of modern variation, but diet nonetheless contributed to differentiating fossil and modern assemblages. Mixed-feeders peaked at non-analog highs between 5 and 3 million years ago and declined to non-analog lows between 2 and 1 million years ago, while grazers exhibited the opposite pattern.

By around 700,000 years ago, almost all fossil communities fell within the modern range of variation for all trait categories. Notably, these functionally modern large-herbivore

assemblages emerged well before taxonomically modern ones — those containing the species present in Africa today — which only appeared during the last ~12,000 years, post-Pleistocene. This means that the emergence of functional modernity does not simply reflect the substitution of extant species for extinct ones but is rather the result of environmental changes that have been playing out for millions of years. Chief among these changes was the steady expansion of C_4 grasslands starting around 3.5 million years ago, which is implicated in the long-term decline of megaherbivores and the rise of grazers relative to browsers and mixed-feeders. Yet, progressive grassland expansion alone is insufficient to explain some of the more recent nonlinearities in community composition. A second contributing factor identified by Faith and colleagues [4] is the increased frequency and severity of dry spells since the mid-Pleistocene. Large-bodied herbivores, non-ruminants, and grazers all tend to be highly water-dependent and hence drought-sensitive [8], and all three of these groups have declined over the last million years.

Faith and colleagues [4] conclude that ancient ecosystems functioned differently to modern ones, which is undoubtedly true. The long-term trends in atmospheric CO_2, extent of C_4 grasslands, and aridity that appear to have caused the changes in large-herbivore communities [4,9] are themselves sufficient to support such an inference. But pinpointing exactly how the non-analog ancient megafauna contributed to causing such differences in ecosystem function is a daunting task.

In attempting detailed reconstructions of ecological prehistory, we have little choice but to try to work backwards from our understanding of modern ecosystems. With most of the world stripped of its megafauna, it is tempting to view modern African protected areas as reference points for large-mammal-dominated Pleistocene and pre-Pleistocene ecosystems — not just in Africa, but worldwide [10,11]. Abundant research shows that large herbivores — and especially megaherbivores — have profound direct and indirect effects on plants, small animals, fire regimes, and ecosystem functions such as nutrient cycling and carbon storage [7,10–15]. The functional differences between modern and ancient large-herbivore communities documented by Faith and colleagues [4] highlight a crucial question: how far can we go in extrapolating from the present to the past?

The megaherbivore trends provide the clearest basis for hypothesis development. The decline in megaherbivore richness — some paleocommunities had more than ten co-occurring species, whereas modern African ecosystems have a maximum of five [9] — mainly affected browsers and mixed-feeders. Based on experimental studies of modern mixed-feeding megaherbivores such as elephants, we can conjecture that ancient ecosystems had greater spatial turnover in tree diversity and higher rates of tree toppling [16]. Tree toppling affects the availability of habitat for small animals [17] as well as the visibility within those habitats, which may have influenced the predator-avoidance strategies of ungulates and hominins [18]. Large trees with large fruits, dense wood, big spines, and tough leaves may have been particularly abundant [15,19]. Ancient ecosystems would have been coupled — for example, via the dispersal of nutrients and seeds — over much longer length scales than occurs today [11].

In developing and testing such hypotheses, however, we must confront the implications of the finding of Faith and colleagues [4] that, "compared to the present, fossil communities occupy a considerably larger amount of functional trait space." If the ecological effects of large herbivores are contingent on the suite of functional traits represented in the community, then simple predictions based on modern research may be misleading. The encouraging news is that although the combinations of traits in ancient herbivore assemblages are non-analog, the traits themselves are still present, at least for the moment. The ability to reliably deduce the environmental impacts of animals from their functional traits is a challenge that ecologists are still struggling with. But we have a rapidly expanding arsenal of tools available to dissect this problem, which are yielding increasingly fine-grained insights into how the phylogeny, morphology, and physiology of extant megafauna influence their diets [20] and their roles within ecosystems [10,14]. With creativity and persistence, we may be able to translate this knowledge in ways that illuminate the history of megafauna past while also helping to safeguard the existence of megafauna future.

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Decision Making: How Is Information Represented in Orbitofrontal Cortex?

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Classically, specific orbitofrontal cortex (OFC) neurons are thought to represent attributes of specific decision options. A new model proposes instead that OFC neurons represent whichever option is currently attended. A recent study, however, tests these two models and rules out the 'current-focus-of-attention' model.

A large amount of experimental evidence indicates that the orbitofrontal cortex (OFC) represents the value of specific options that are available in the environment [1–5]. Over the last decade, the group of Padoa-Schioppa has used a simple economic task in which monkeys choose between different juice rewards to investigate the specific contributions of the OFC to value-based decisions [3]. They found three functional classes of neurons in OFC that can be interpreted as the inputs and outputs of a comparison process on which decisions are based. Importantly, these functional cell types are stable across decisions regarding different types of juice [6]. These experiments indicate that specific OFC neurons have a dedicated and stable function within the decision process, likely due to their specific connections within the local circuitry. These connections provide a labeled-line framework that clearly links the information that is represented in a neuron with the relevant option. The value of both options is represented simultaneously by different groups of OFC neurons. This allows for the comparison process to take place. Both of these conclusions seem straightforward and intuitive. Nevertheless, both of them have been put into question by recent experiments from a number of other labs. However, a new study from Ballesta and Padoa-Schioppa, published in a recent issue of *Current Biology*, shows that while attention strongly modulates OFC activity, the basic framework of value representations is using labeled lines [7]. This strongly argues against a new radically different model of the OFC.

In one set of studies, monkeys were tested with options that were presented sequentially [8–10]. In parallel, researchers have started to study the role of attention in value-based decision making [11–13]. These two independent lines of research recently inspired a radically different model of value-based decision making [14]. This new model is based on the principles of foraging theory [15] and suggests that a sequential process underlies value-based decisions. According to this model, OFC represents only the attributes of one attended option, even if multiple options are present concurrently. The attended option will be either accepted or rejected. Rejection leads to the shift of attention to another option until an option is accepted and can include revisiting a previously rejected option. Importantly, the option to which OFC neurons refer is determined dynamically by attention and not stably by labeled lines. Accordingly, comparison results not from explicit competition between discrete neuron populations.