

# The Mammoth Steppe: A Frosty Savanna

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## Abstract

This study investigates the potential of using contemporary African Grasslands as an ecological analog to understand the Pleistocene Eurasian Mammoth Steppe, a complex ecosystem known primarily through estimations, proxies, and extrapolation of the limited direct evidence. By examining the themes of climate, flora, and fauna, the research aims to assess the validity of African Grasslands in offering insights into the dynamics of the Mammoth Steppe, particularly in the context of megafaunal interactions. Despite the inherent challenges of employing proxies, this analysis highlights significant, albeit inconsistent, parallels between the two ecosystems, such as bioproductivity and mammalian biodiversity. Results indicate that while the African Grasslands cannot serve as a comprehensive proxy for the Mammoth Steppe, they present a valuable opportunity for generating hypotheses and stimulating further research on megafaunal impacts during the Pleistocene. The findings underscore the necessity for cautious application of proxy methods in paleoecological studies, emphasizing the importance of establishing independent comparisons to enhance the scientific understanding of extinct ecosystems. This work lays the groundwork for future investigations into the relationships between existing and extinct ecological systems.

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## Introduction

The Mammoth Steppe was a massive ecosystem characterized by low temperatures and the presence of megafauna. However, certain aspects of this ecosystem cannot be directly studied through physical remains, necessitating the use of inferred information. This study aims to investigate and scientifically ground the practice and methodology of leveraging existing ecosystems to gain insights into extinct ones in the fields of archaeology, paleoecology, and paleontology. Specifically, it explores how the Holocene Grasslands in Eastern and Southern Africa, referred to as the African Grasslands (AG), can provide well-founded inferences about the Pleistocene Eurasian Mammoth Steppe (MS), with a focus on the influence of megafauna.

The choice of the savanna ecosystem for this study is not arbitrary, as previous research (such as Larramendi, 2016; Palombo et al., 2005) has utilized animals from both the African Grasslands and the Mammoth Steppe in comparative faunal studies. This demonstrates an existing scientific interest in using components of the African grasslands as proxies for the Mammoth Steppe. Moreover, both ecosystems share the common characteristic of hosting megafauna, while modern Eurasia lacks megafauna except for Asian elephants.

The presence of megafauna is a crucial factor in considering the African Grasslands as a potential ecological proxy for the Mammoth Steppe. However, the term "megafauna" lacks a clear and universally accepted definition within the scientific community. Its definition varies depending on the focus of each study. Stuart (1991) defined megafauna as land animals surpassing certain mass thresholds, the most conservative of which was  $\geq 1000\text{kg}$ . Generally, domesticated animals are excluded from this definition.

The focus of this paper is the Mammoth Steppe in the Middle and Late Pleistocene ages, spanning approximately 800kya to 12kya. In contrast, the African Grasslands are examined within the context of the Holocene epoch, which encompasses the time frame from 12kya to the present day.

***As environments characterized by the presence of megafaunal animals, to what degree do African Grasslands possess potential as an ecosystem-wide proxy for studying the Mammoth Steppe?***

Following a brief discussion of methodology, this question will be examined through the comparison of three themes: Climate, Flora, and Fauna. Each of these sections will compare environmental data and establish judgments on the potential for using the African Grasslands as an analog ecosystem.

## Methodology

In the context of this project, a proxy or analog refers to a more accessible subject of study that can be used to draw inferences about a less accessible subject. Specifically, the African Grasslands serve as a readily accessible living ecosystem compared to the Mammoth Steppe.

It is important to note that a proxy is valuable not as standalone evidence, but as a tool that supports other evidence. For example, herding behavior in mammoths currently lacks direct non-proxy evidence. To establish such behavior in mammoths, other evidence would be necessary, which could be supported by our understanding of elephant behavior. A good proxy can also catalyze research, for instance studying elephant behavior may uncover types of evidence that can be sought to prove or disprove herding behavior in mammoths.

When evaluating a proxy, its quality can be determined by scientifically verifiable similarities and differences between the proposed analogs. For instance, elephants serve as high-quality analogs of mammoths when studying diet because mammoth diet can be verified through dental isotope analysis and dental wear patterns. These findings can be compared to our understanding of elephant diet.

Assessing the quality of the African Grasslands as a proxy involves comparing various ecological aspects to what is known about the Mammoth Steppe. The closer the match between these aspects, the higher the quality of the proxy.

### **Caveats**

Knowledge about the Mammoth Steppe heavily relies on analogs and proxies since direct measurements are rarely available. Consequently, our understanding of the Mammoth Steppe as a past ecosystem is primarily based on estimations.

To address this limitation, the study incorporates possible surviving refugia that closely resemble the Mammoth Steppe in terms of climate, flora, and surviving fauna. These refugia include the Altai-Sayan (Pavelková Řičánková et al., 2014), North-Eastern Siberia, Central Alaska, and the Yukon Territory (Zimov et al., 2012). They will be used to supplement estimations of the Mammoth Steppe. Rigorous scrutiny has also been applied to ensure the integrity of these estimations. However, it is important to approach assertions regarding the Mammoth Steppe with skepticism.

The African Grasslands have been chosen as a potential proxy over these refugia due to their lack of megafauna, biodiversity, and bioproductivity that the Mammoth Steppe is believed to have had. While

these refugia may initially seem like better candidates, a closer examination reveals a different perspective, which will be discussed in more detail.

## Climate

In this subsection on climate, a comparison will be made between temperature and precipitation measurements of three representative African Grassland ecosystems and the established refugia of the Mammoth, along with estimations based on direct data from the Mammoth Steppe. The sources providing information on temperature and precipitation in modern ecosystems can be found in Annex A.

### Temperature

<b>Table 1.</b>	<b>Average Annual Temperature High</b>	<b>Average Annual Temperature Low</b>	<b>Greatest Deviations from Annual Average</b>
<b>Serengeti</b>	26.0°C	14.7°C	+1.2°C   -1.8°C
<b>KwaZulu-Natal</b>	24.8°C	11.3°C	+5.0°C   -5.5°C
<b>Ngorongoro Crater</b>	21.7°C	11.4°C	+1.0°C   -1.9°C
<b>Altai-Sayan</b>	11.6°C	-2.1°C	+15.3°C   -17.8°C
<b>North-East Siberia</b>	-6.1°C	-17.3°C	+24.7°C   -23.3°C
<b>Central Alaska</b>	0.3°C	-12.9°C	+23.4°C   -22.2°C
<b>Yukon Territory</b>	2.4°C	-9.8°C	+19.7°C   -21.8°C

*Table 1. Average temperature data from AG representatives against MS refugia*

This table compares temperature differences between African Grasslands and the refugia of the Mammoth Steppe. The refugia exhibit significantly colder temperatures, leading to frequent sub-zero temperatures and water freezing. Freezing cycles have severe consequences, including reduced plant growth and decreased nutritional availability during cold periods. The extreme seasonality is highlighted by monthly deviations from the annual average temperature. African Grasslands show minimal temperature fluctuations, with up to an average monthly range of 6°C, while the refugia experience deviations ranging from 15°C to nearly 25°C. Organisms in the refugia must possess adaptations to survive across a wide range of temperatures. According to Zimov et al. (2012), the Mammoth Steppe had lower summer temperatures (8°C to 10°C), making it unlikely that the African Grasslands can serve as a proxy based on temperature alone.

## Precipitation

<b>Table 2.</b>	<b>Average Total Annual Precipitation</b>	<b>Average Wet Quarter Precipitation</b>	<b>Average Dry Quarter Precipitation</b>
<b>Serengeti</b>	881mm	376mm	66mm
<b>KwaZulu-Natal</b>	844mm	371mm	48mm
<b>Ngorongoro Crater</b>	3,480mm	2,055mm	34mm
<b>Altai-Sayan</b>	570mm	274mm	36mm
<b>North-East Siberia</b>	239mm	111mm	31mm
<b>Central Alaska</b>	270mm	147mm	23mm
<b>Yukon Territory</b>	153mm	68mm	14mm

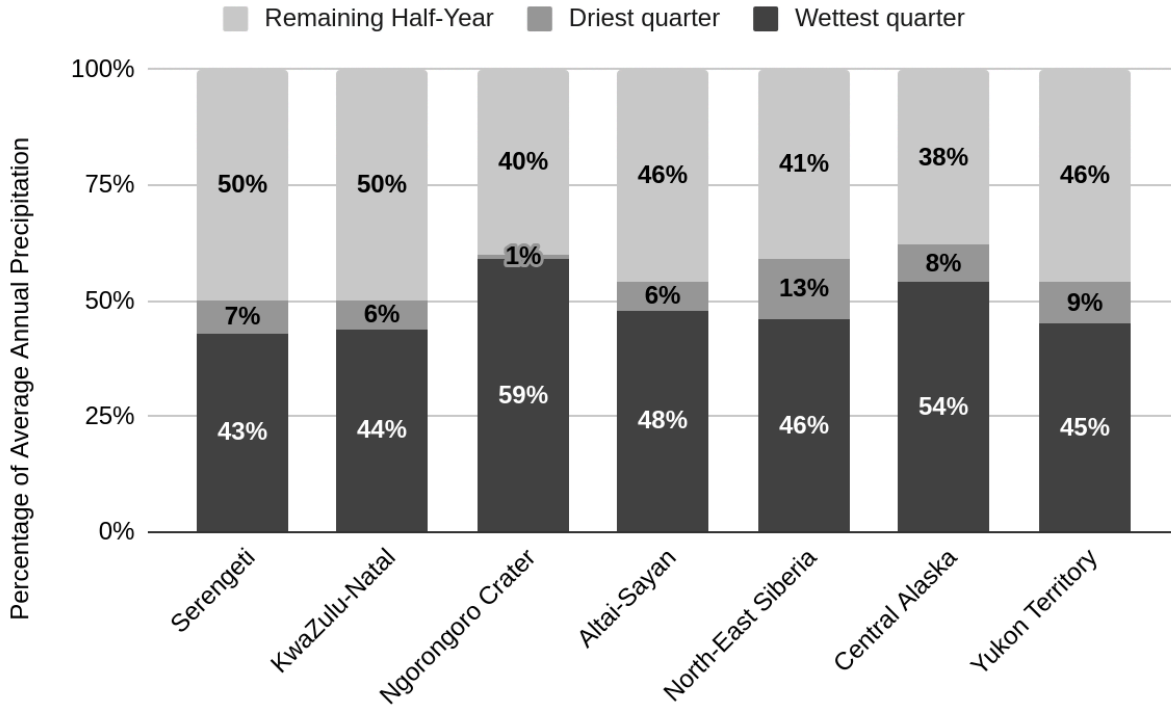
*Table 2. Average precipitation data from AG representatives against MS refugia*

The table shows that African Grasslands receive higher annual precipitation compared to the refugia. However, it should be noted that snowfall is not consistently included in precipitation measurements, which increases water availability in the environment. Conversely, water evaporation reduces the amount of availability, this process is more impactful in the African Grasslands (House & Hall, 2001). It is reasonable but not conclusive to state that the refugia have similar annual water availability as the African Grasslands.

Zimov et al. (2012) and Velichko and Zelikson (2001) estimated that the Mammoth Steppe received 100mm to 300mm of annual precipitation, which aligns with the refugia but differs from the African Grasslands. Despite the lower precipitation, evidence of ancient lakes suggests that the Mammoth Steppe likely had lower total annual water evaporation, and therefore comparable water availability to the African Grasslands.

Figure 1 (below) displays precipitation density throughout the year, allowing for a comparison of seasonality. The wet quarter represents the three consecutive months with the highest shared rainfall,

while the dry quarter represents the three months with the lowest shared rainfall. It's important to note that the specific months comprising these quarters vary by region.



**Figure 1.** Share of Regional Annual Precipitation by Annual Quarter

Regarding seasonality, the wet quarter typically accounts for approximately 48% (ranging from 43% to 59%) of the annual precipitation in all these regions, while the dry quarter represents roughly 7% (ranging from 1% to 13%). This data suggests that the African Grasslands and refugia may have similar periodicity in terms of annual precipitation. However, it remains inconclusive. To make a definitive conclusion, a larger dataset encompassing various ecosystems would be necessary to examine the possible ranges of precipitation seasonality comprehensively and determine whether the refugia align with the African Grasslands in this aspect.

Generating comprehensive data for the precipitation seasonality of the Mammoth Steppe is indeed challenging, and the existing literature lacks evidence based primarily on paleoecological data. In this case, no definite conclusions can be drawn regarding the Mammoth Steppe.

In this climatic comparison, the limited available evidence does not strongly support the African Grasslands as a reliable proxy for the Mammoth Steppe. Further evidence may change this assessment.

# Floral Diversity & Distribution

## Bioproductivity

Productivity, defined as the rate of biomass production by individuals, populations, or communities, is a crucial ecological factor (OED, 2023). Highly productive ecosystems can support more organisms, including larger and more complex ones. The mechanisms underlying high bioproductivity are intricate and go beyond the scope of this paper.

House & Hall (2001) describe Tropical Savannas, which are part of the African Grasslands, as highly productive environments. This conclusion is based on biomass measurements, the presence of large herbivores, and the dominance of grasses in the ecosystem.

Regarding the Mammoth Steppe, Zimov et al. (2012) focus on establishing its similarity to biomes like the African Grasslands in terms of biomass and bioproductivity. Despite the low temperatures and precipitation, they find that the Mammoth Steppe's animal biomass and plant productivity were comparable to an African savanna. This conclusion is supported by permafrost-preserved soil in Alaska, which holds the largest amount of organic carbon in the past and present and belonged to the same ecosystem as the Mammoth Steppe. The authors also argue for high bioproductivity based on the substantial biomass attributed to herbivores, suggesting that such herbivory levels could only be sustained by an ecosystem with extremely high bioproductivity.

## Grasses

Zimov et al. (2012) demonstrate a correlation between periods of abundant grasses and high populations of now-extinct Mammoth Steppe fauna. They observe a gradual decline in grass abundance and a corresponding scarcity of Mammoth Steppe megafauna as the ecosystem transitioned to its Holocene existence. This highlights the vital role of grasses in the Pleistocene Mammoth Steppe ecosystem. The authors propose a complex feedback loop in which megafaunal grazing behavior prevents non-grass vegetation from dominating the ecosystem, allowing grasses to thrive. In turn, the megafauna rely on these grasses for nutrition (Zimov, 2005). The paper establishes that the extinction of megafauna was not primarily caused by climate change but rather by human-induced reduction in megafaunal populations. This reduction allowed for increased tree growth, resulting in reduced resources for the megafauna, thus perpetuating a feedback loop.



House & Hall (2001) emphasize the importance of grasses not only for the megafauna of the African Grasslands but also for the maintenance of grass extent through the behavior of animals such as elephants, which remove competing trees.

## Subregional Environments

Palynological data from Pleistocene coring across Eurasia reveals that the Mammoth Steppe comprised a range of environments, including steppe-like grasslands, tundra, marshes, coniferous forests, deciduous forests, and possibly deserts (Field et al., 2000; Zimov et al., 2012).

Field et al. (2000) provides insights into the biomes present in the Isère department of France based on palynological core data. Their findings suggest that the area had heavy forestation, with approximately half of it consisting of temperate deciduous forests, along with coniferous forests, taiga, and mixed forests. A cool steppe environment was also inferred, although to a lesser extent. The presence of conifers, specifically species from the *Abies*, *Picea*, and *Pinus* genera, was prominent. Additionally, there were indications of broadleaf trees, including *Ulmus*, *Quercus*, *Fagus*, and *Salix*, although in smaller quantities.

The African Grasslands exhibit similar characteristics, with open grassy areas and varying densities of forests (House & Hall, 2001). The key difference lies in the plant composition. Conifers, or gymnosperms in general, are less common in the African Grasslands compared to the Mammoth Steppe. However, both ecosystems encompass a variety of deciduous trees.

Despite differences in climate, the botanical and environmental aspects of the African Grasslands and the Mammoth Steppe are remarkably similar. Both ecosystems are dominated by grasses while maintaining plant diversity and the presence of forests. They share a heterogeneous nature in terms of their composition.

# Fauna

## Mammalian Biodiversity

Biodiversity is crucial for comparing ecosystems, especially in terms of mammalian diversity. Previous research by van Ruijven and Berendse (2005) established a positive correlation between ecosystem productivity and biodiversity, applicable in this context. Sahney et al. (2010) used a common method in biology and ecology, tallying taxa within a geographic range to measure biodiversity.

Due to limited ecological studies in the region (House & Hall, 2001), obtaining precise numbers on mammalian species in the African Grasslands is challenging. Nevertheless, Turner & Antón (2004) identified approximately 1100 mammal species across Africa, extending beyond the African Grasslands. According to a variety of sources, the Serengeti, a part of the African Grasslands, hosts at least 24 endangered mammals (UNESCO, 1981), 35 large mammals (Encyclopaedia Britannica, 2023), and over 70 large mammal species according to the Serengeti Park (2023) website. East Africa is widely recognized as the region with the highest mammalian biodiversity on Earth, although specific figures are lacking (McClanahan, 1996).

Regarding the Mammoth Steppe, several papers (Bocherens, 2015; Guthrie, 1982, 2001; Larramendi, 2016; Zimov et al., 1995, 2012; Zimov, 2005) mention its unexpectedly high mammalian diversity without providing figures for comparison. In the final section of this paper, titled "Faunal Comparisons," I present a list of 13 mammal species found in the Mammoth Steppe, though it is not exhaustive. Considering additional mammal species mentioned in the aforementioned studies, there are at least 15 more mammal species. This conservative estimate suggests a total of 28 large mammal species, comparable to the estimated values for the Serengeti.

These findings, supported by extensive research, strongly indicate that both the Mammoth Steppe and the African Grasslands boast similarly high levels of mammalian biodiversity.

## Faunal comparisons

The paper's final section compares the fauna of the Mammoth Steppe with analogous species from the African Grasslands. Analog species were chosen based on phylogenetic relatedness and some similarities in diet or known behavior.

The analogs are assessed in terms of body mass, diet, and ecological niche. Body mass provides insights into environmental impact, predation potential, population size, and nutritional needs. Diet itself is evidence and indicates variations in subsistence strategies. Ecological niche summarizes the role of a taxon in its environment. For extinct taxa, it is determined by physiological characteristics like teeth, size, and diet. Additionally, inferring niche solely based on phylogenetic relation can be misleading, as shown by the Cave Bear initially mistaken for an apex predator but later found to be herbivorous (Zimov, 2005).

In the following tables, Mammoth Steppe taxa are in bold, with † indicating extinct taxa. Although some Mammoth Steppe taxa still exist, they are compared to African Grassland analogs due to the absence of megafauna in their native ecosystems.

Data on African Grassland taxa and non-extinct Mammoth Steppe taxa's body masses, diets, and niches are from the Animal Diversity website, supplemented with Pleistocene specimens when available (marked with <sup>P</sup>). Clarified sources can be found in the references section and Annex B.

<b>Table 3a.</b>	<b>Body Mass</b>	<b>Diet</b>	<b>Niche</b>
<i>Loxodonta</i>	2.0t - 6.1t	Grasses, fruits, herbs, foliage, wood	Flexible Grazer & Browser
† <i>Palaeoloxodon antiquus</i>	11.5t	Foliage, wood, grasses	Flexible Browser & Grazer
† <i>Mammuthus</i>	3.0t - 11.5t	Herbs, grasses	Flexible Grazer
<i>Ceratotherium</i>	1t - 3.6t	Foliage, herbs, grasses	Flexible Grazer
<i>Diceros</i>	0.8t - 1.4t	Foliage, herbs, grasses, wood	Flexible Grazer
† <i>Coelodonta</i>	1.5t	Grasses, foliage	Flexible Grazer
† <i>Elasmotherium</i>	4t - 5t	Grasses, foliage	Specialized Grazer
<i>Syncerus</i>	0.3t - 0.9t	Grasses	Specialized Grazer
† <i>Bos primigenius</i>	0.7t - 1.5t	Grasses, foliage	Flexible Grazer

*Table 3a. Megafaunal Comparison*

*Loxodonta* (African Elephant) is considerably less massive than *P. antiquus* (Straight-Tusked Elephant), but the difference in body mass between *Loxodonta* and *Mammuthus* (Mammoth) is less significant. Their diets exhibit similarities but with distinct preferences. Furthermore, their ecological niches overlap considerably. This data suggests that *Loxodonta* could serve as a reasonable general analog for *Mammuthus*. However, due to the notable difference in body mass, *Loxodonta* may not be a suitable analog for *P. antiquus*.

*Ceratotherium* (White Rhinoceros) and *Diceros* (Black Rhinoceros) closely align with *Coelodonta* (Woolly Rhinoceros) and *Elasmotherium* in all measured aspects. The primary distinction lies in their food preferences, with evidence suggesting *Elasmotherium* had a specialized diet (Boeskorov, 2012; van der Made & Grube, 2010). However, this difference could potentially be accounted for by studying a population of *Ceratotherium* that primarily consumes grasses.

*Syncerus* (African Buffalo) also aligns well with *B. primigenius* (Aurochs) in all measured aspects. Nonetheless, it's important to note that the diet and niche source for *B. primigenius* (Heptner et al., 1988) assumed its diet would be similar to cattle, which does not provide direct evidence. Consequently, the comparison between *Syncerus* and *B. primigenius* effectively becomes a comparison between *Syncerus* and the extant *B. taurus* (Cattle), making this data unsuitable for testing analog potential.

<b>Table 3b.</b>	<b>Body Mass</b>	<b>Diet</b>	<b>Niche</b>
<i>Connochaetes</i>	110kg - 270kg	Grasses, foliage, wood	Flexible Grazer
<sup>P</sup> <i>Rangifer</i>	55kg - 320kg	Lichens, grasses	Specialist Grazer
<sup>P</sup> <i>Ovibos</i>	180kg - 400kg	Foliage, wood	Flexible Browser
<i>Eudorcas thomsonii</i>	15kg - 35kg	Grasses, foliage, wood	Flexible Grazer & Browser
<sup>P</sup> <i>Saiga</i>	30kg - 45kg	Lichens, grasses	Flexible Grazer
<i>Cervus elaphus</i>	70kg - 500kg	Foliage, wood, lichens	Flexible Browser & Grazer

**Table 3b.** Non-Megafaunal Herbivore Comparison

The mass ranges of the analog *Connochaetes* (Wildebeest) compared to *Rangifer* (Reindeer) and *Ovibos* (Musk Ox) show some alignment, although not perfect. Additionally, their diets exhibit distinct

differences. This suggests that *Connochaetes* may not be the ideal analog for Pleistocene *Rangifer* and *Ovibos*, but it does not necessarily make it a poor analog.

Regarding *E. thomsonii* (Thomson’s Gazelle), its mass aligns well with the Pleistocene *Saiga*, but poorly with the mass of a Holocene *C. elaphus* (Red Deer). However, the diets and niches of the analog and Mammoth Steppe taxa demonstrate significant alignment, particularly for *C. elaphus*. Based on this data, it can be argued that *E. thomsonii* serves as a high-quality analog for the Pleistocene *Saiga*, but its suitability as an analog for *C. elaphus* is questionable.

<b>Table 3c.</b>	<b>Body Mass</b>	<b>Diet</b>	<b>Niche</b>
<i>Panthera leo</i>	120kg - 280kg	Large (non-megafaunal) herbivores, juveniles, small animals	Apex generalist pack predator, scavenger
† <i>Panthera spelaea</i>	270kg - 340kg	Large herbivores, Megafaunal juveniles	Apex generalist solitary predator, (scavenger?)
† <i>Homotherium</i>	≤ 190kg	Megafaunal juveniles, large herbivores	Apex specialized pack predator, (scavenger?)
<i>Crocota crocuta</i>	45kg - 80kg	Large (non-megafaunal) herbivores, juveniles, small animals, bones	Apex generalist pack predator, scavenger
<i>Hyaena hyaena</i>	25kg - 45kg	Carrion, detritus, bones	Non-apex generalist solitary scavenger
† <i>Crocota spelaea</i>	88kg	Large animals, bones	Predator, scavenger
<i>Lycaon</i>	15kg - 40kg	Large (non-megafaunal) herbivores, juveniles	Apex specialist pack predator
<sup>P</sup> <i>Canis lupus</i>	20kg to 80kg	Large herbivores, megafauna, juveniles	Apex generalist pack predator, scavenger

**Table 3c.** Carnivore Comparison

The mass of *P. leo* (African Lion) differs significantly from that of *P. spelaea* (Cave Lion) but closely matches that of the more distantly related *Homotherium*. Their diets align almost perfectly. While

megafauna are not typically part of the diet of *P. leo*, there is evidence suggesting that *P. leo* can hunt *Loxodonta* (Joubert, 2006). The main difference lies in pack behavior, with *P. spelaea* speculated to be a solitary hunter due to its mass being similar to its prey (Bocherens et al., 2011), whereas there is evidence of pack behavior in *Homotherium* (Metcalf, 2011). If this is the case, then *P. leo* would serve as a perfect analog for *Homotherium* and a less optimal one for *P. spelaea*.

The available non-proxy data on *C. spelaea* (Cave Hyena) is limited, with research (Rivals et al., 2022) indicating it is effectively identical to *C. crocuta* (Spotted Hyena), except for minor cranial morphological differences. While it cannot be conclusively established that *C. crocuta* is a good analog for *C. spelaea*, it is undoubtedly a better analog than *H. hyaena* (Striped Hyena), which differs significantly across all three criteria.

Regarding *Lycaon* (African Wild Dog), it is not a perfect analog but still has some value for Pleistocene *C. lupus* (Grey Wolf). Their mass aligns well, although not perfectly. However, there is no evidence of *Lycaon* hunting or scavenging on megafauna, despite coexisting with them. In contrast, there is clear evidence of Pleistocene *C. lupus* as a megafaunal hunter (Leonard et al., 2007). Despite the phylogenetic distance and the difference in body mass, *P. leo* could be considered a more suitable analog for Pleistocene *C. lupus*.

In summary, several potentially high-quality analog taxa from the African Grasslands can be identified for Mammoth Steppe taxa. However, accessing the required data for making these comparisons can be difficult, and in some cases, the data may not exist. Nevertheless, this non-exhaustive proof-of-concept comparison highlights the potential of using African Grassland fauna as analogs for certain Mammoth Steppe fauna.

## Conclusion

The Mammoth Steppe is predominantly known through estimations and proxies. Validating a proxy requires comparing two independent systems. Consequently, assessing the African Grasslands as an analog of the Mammoth Steppe, in terms of proxy potential, is highly challenging and potentially impossible. Utilizing proxies to study proxies will inevitably result in false positives. Thus, my aim in this research has been to minimize such instances and explicitly acknowledge when they were unavoidable.

The African Grasslands cannot be regarded as a comprehensive ecosystem-wide proxy for the Mammoth Steppe, and it is unlikely that such a proxy exists for any pair of ecosystems. However, within the context

of studying the impact of megafauna during the Pleistocene, the African Grasslands offer the most suitable option for comparison, generating hypotheses, and stimulating further research. My findings demonstrate a significant but non-universal level of consistency between various aspects of these two ecosystems.

This paper provides a broad examination that touches upon multiple topics, but each section could potentially be expanded into a separate research article. Nevertheless, this research establishes a foundation for considering the African Grasslands as a proxy ecosystem for the Mammoth Steppe, and I anticipate further investigations in this field.

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## Annex A - Climate Sources

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## Annex B - Fauna Sources

- *Palaeoloxodon* & *Mammuthus* masses from Larramendi (2016)
- *Palaeoloxodon* diet & niche from Palombo et al. (2014)
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- *Coelodonta* mass, diet and niche from from Boeskorov (2012) and van der Made & Grube (2010)
- *Elasmotherium* mass from Zhegallo et al. (2005)
- *Elasmotherium* diet & niche from van der Made & Grube (2010)
- *Bos primegenius* mass from Van Vuure, C. (2005)
- *Bos primegenius* diet and niche Heptner et al. (1988)
- *P. spelaea* mass, diet, and niche from Bocherens et al. (2011)
- *Homotherium* mass from Sorkin (2008)
- *Homotherium* diet & niche from Metcalfe (2011)
- *Crocota spelaea* mass from Sauqué et al. (2017)
- *Crocota spelaea* diet & niche from Rivals et al. (2022)
- Pleistocene *Saiga* diet & niche from Jürgensen et al. (2017)
- Pleistocene *Rangifer* diet & niche Rivals et al. (2020)
- Pleistocene *C. Lupus* diet & niche from Leonard et al. (2007)
- All other data concerning mass, diet, and niche from <https://animaldiversity.org/>