

Megafaunal isotopes reveal role of increased moisture on rangeland during late Pleistocene extinctions

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The role of environmental change in the late Pleistocene megafaunal extinctions remains a key question, owing in part to uncertainty about landscape changes at continental scales. We investigated the influence of environmental changes on megaherbivores using bone collagen nitrogen isotopes ($n=684$, 63 new) as a proxy for moisture levels in the rangelands that sustained late Pleistocene grazers. An increase in landscape moisture in Europe, Siberia and the Americas during the Last Glacial-Interglacial Transition (LGIT; ~25–10 kyr BP) directly affected megaherbivore ecology on four continents, and was associated with a key period of population decline and extinction. In all regions, the period of greatest moisture coincided with regional deglaciation and preceded the widespread formation of wetland environments. Moisture-driven environmental changes appear to have played an important part in the late Quaternary megafaunal extinctions through alteration of environments such as rangelands, which supported a large biomass of specialist grazers. On a continental scale, LGIT moisture changes manifested differently according to regional climate and geography, and the stable presence of grasslands surrounding the central forested belt of Africa during this period helps to explain why proportionally fewer African megafauna became extinct during the late Pleistocene.

The relative roles of human impacts and environmental change in the extinction of the late Pleistocene megafaunal communities of Eurasia and the Americas during the LGIT, approximately 25–10 kyr BP (thousand years before present), remain poorly understood. Rapid warming events have recently been linked with megafaunal extinctions, both with and without the synergistic effects of human presence^{1,2}. However, the apparently less severe impacts of previous glacial–interglacial cycles remain difficult to explain, and the potential role of human hunting is also complicated by the long-term coexistence of megafauna with early modern human and Neanderthal hunters in both Africa and Eurasia. A crucial question in this debate is the nature and extent of the landscape changes during and after the Last Glacial Maximum (LGM, ~25–15 kyr BP) which accompanied extinction events in different parts of the world^{3,4}. These changes can be caused by altered climate, human activities and the presence of megafauna, all of which exert strong top-down pressure on the vegetation, soil and nutrient cycling processes at the base of the food chain. These interactions can be detected through direct evidence (for example butchery marks on bones) or indirect methods such as relating the timing of climate events to extinction events in the palaeontological record^{1,3}. Direct evidence approaches are particularly important in establishing causality, and studies of fossil abundance, body size and dietary stable isotopes have all identified environmental factors directly impacting megafaunal ecology^{5–7}.

Megaherbivores played a critical role in Pleistocene ecosystems, functioning as ‘nutrient pumps’⁸, adapted to harvesting and distributing the nutrients available across widespread rangelands such as the mammoth steppe, a grass/forb-dominated biome extending from Europe to Siberia and across the Bering Land Bridge into northwestern North America^{4,9,10}. Rangelands and grazers were interdependent, with megafauna impeding the colonization of trees through trampling and sapling consumption, while clearing and breaking down the organic matter from seasonally senescing foliage⁹. Seasonal aridity also strongly influences the distribution of rangelands, such that climate change can exert extinction pressure on megafaunal rangeland grazers through habitat loss and range fragmentation^{9,11–13}. Rangelands are particularly amenable to the study of moisture-driven environmental change through nitrogen isotopes preserved in grazer fossils, for which a strong inverse correlation exists between soil moisture and the heavier nitrogen stable isotope ¹⁵N relative to ¹⁴N (expressed using delta notation, $\delta^{15}\text{N}\%$) in soils, plants and herbivore collagen¹⁴. The relationship is most pronounced where annual rainfall is lower than 500–700 mm (refs ^{14,15}), which is typical for grassland biomes, and the probable range for those in the late glacial leading into the dry LGM^{16,17} (Supplementary Fig. 17, Supplementary References 5). Palaeoisotopic studies have detected LGIT decreases in $\delta^{15}\text{N}$ values across the mammoth steppe, which have been related to moisture from increasing precipitation and degrading permafrost^{5,12,16,18–20}. The changes in $\delta^{15}\text{N}$ values

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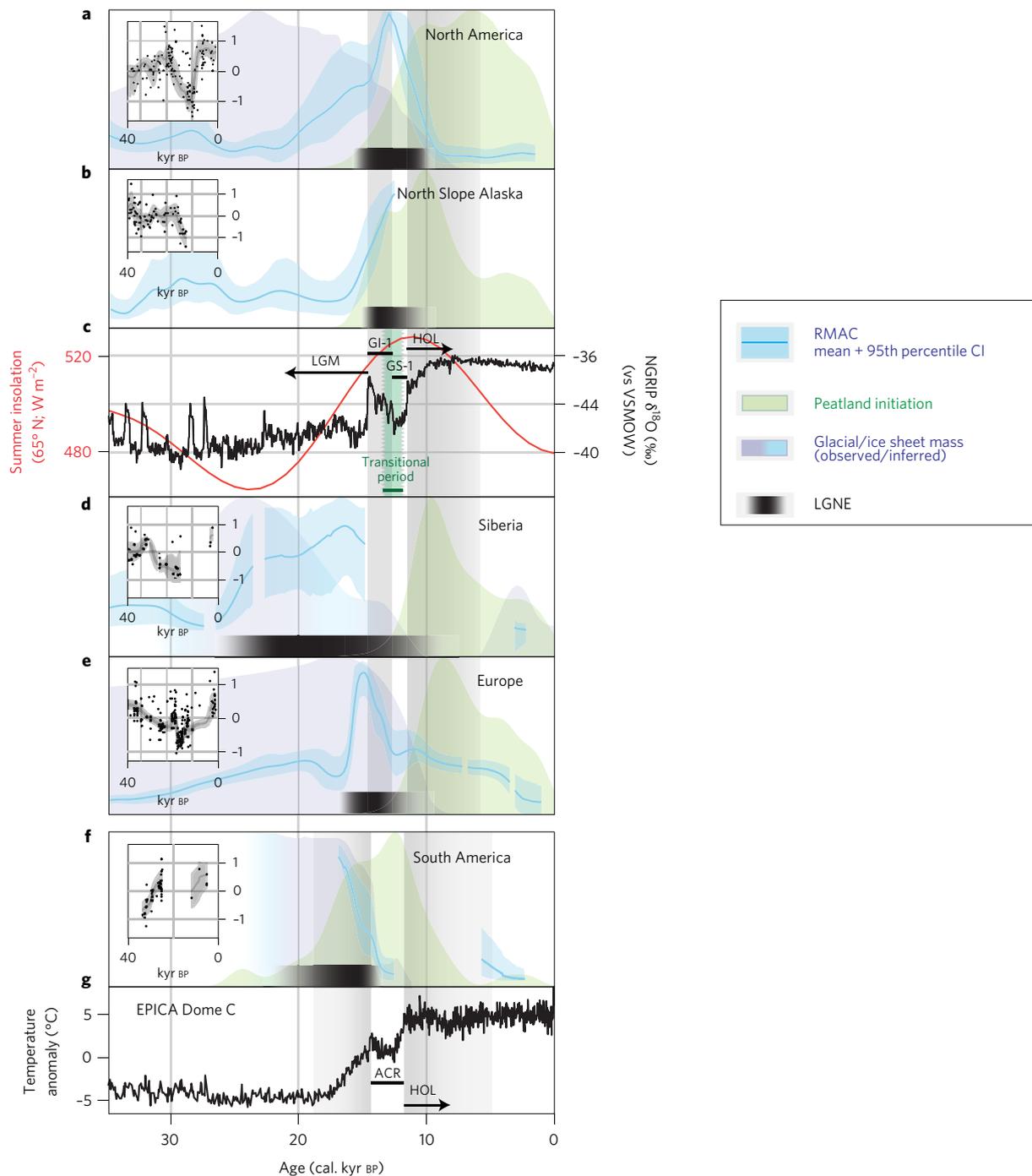


Figure 1 | Reconstructed moisture levels. **a–g**, The moisture levels are given as RMAC based on stable isotope values ($\delta^{15}\text{N} (\text{‰}) = \left[\frac{(^{15}\text{N}/^{14}\text{N})_{\text{sample}}}{(^{15}\text{N}/^{14}\text{N})_{\text{air}}} - 1 \right]$) of megafaunal grazers (bison, horse, llama) compared with palaeoclimate, peatland and glacial records for the Northern (**a,b,d,e**) and Southern Hemisphere (**f**), with the approximate timing of the LGNE indicated. **a**, North America (northwestern United States and Canada; $n = 139$); **b**, North Slope Alaska ($n = 131$); **d**, Siberia ($n = 47$); **e**, Europe ($n = 216$); **f**, South America (Patagonia; $n = 45$). The normalized $\delta^{15}\text{N}$ values from which moisture was estimated are shown inset in each panel, with each taxon normalized separately for each region with time on the horizontal axis and standard deviations from the mean on the vertical axis. The data are overlain by the smoother used to produce the RMAC (median ± 95 th percentile CIs, 1,500 bootstraps; see Supplementary Methods). The LGNE is apparent across widely different species and areas. The RMAC is scaled relative to itself, with the median value of 1,500 bootstrap replicates shown with 95th percentile confidence intervals. Peatland initiation rate, represented as the Gaussian kernel density of basal peat core radiocarbon dates, is shown in solid green (Supplementary Methods and Supplementary References), scaled for visualization. Proxies for glacial retreat (**a**, modelled contribution to sea level by North American ice-sheet complex; **c**, multiproxy inferred extent of glaciation in Northern Urals; **d**, modelled volume of Eurasian ice sheet; **f**, modelled volume of Patagonian ice sheet; Supplementary References) are displayed in purple/blue, scaled for visualization and reproduced from figures in original sources. The NGRIP Greenland $\delta^{18}\text{O}$ (vs VSMOW, Vienna Standard Mean Ocean Water) temperature proxy (Supplementary References) is shown in **c**, along with average Northern Hemisphere summertime insolation, and the inferred timing of a ‘temporary optimum’ posited for North America^a; see also Fig. 2b. The EPICA Antarctica temperature proxy (Supplementary References) is shown in **g**, with major warming events indicated: LGM, Last Glacial Maximum; GS-1, Greenland Interstadial/Stadial 1; HOL, Holocene warming; ACR, Antarctic Cold Reversal.

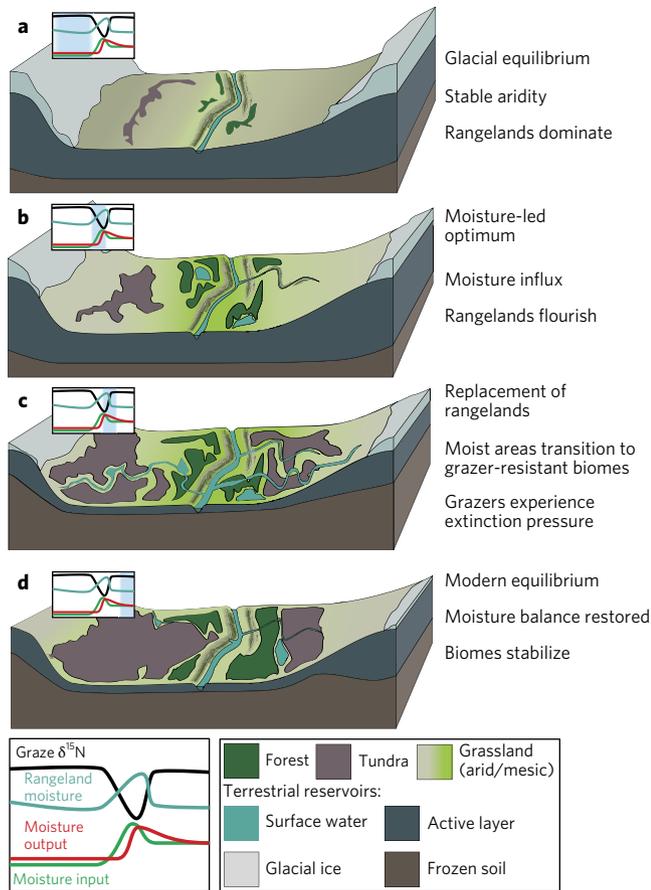


Figure 2 | A series of landscape cartoons illustrating the interaction between $\delta^{15}\text{N}$ values of preferred graze, soil moisture balance and the moisture-boon-replacement model^{9,11,12}. a–d, The green–brown gradient of rangeland corresponds to the increased availability of quality graze in the presence of available soil moisture, and the size of tundra/forest biomes represents the overall dominance of grazer-resistant biome types. Line graphs (top left of each panel) represent the supposed behaviour of $\delta^{15}\text{N}$ values and moisture sources, with the active time period highlighted in blue. The changing depth of the active layer (unfrozen soil) in this example is applicable to far northern tundra and forest biomes underlain by permafrost, in which organic litter insulates soil and decreases the summer thaw depth⁹.

constitute direct evidence that increased moisture altered megafaunal ecology throughout Eurasia and the Americas during this critical period of global climate change, glacial retreat, widespread vegetation change and human migration. Using dated $\delta^{15}\text{N}$ values from herbivores on four continents, we reveal the timing and potentially global scope of moisture influences on megafaunal ecology.

Results

We generated radiocarbon-dated megafaunal collagen $\delta^{15}\text{N}$ values from LGIT rangeland biomes across Eurasia and North and South America, focusing on obligate grazers to avoid the confounding effects of dietary switching (Supplementary Figs 9–11, 18–20). The wide geographical range of sampling sites ensures that the $\delta^{15}\text{N}$ datasets reflect shifts in moisture regimes acting over regional scales. We developed a relative moisture availability curve (RMAC) as a means of visualizing the approximate relative changes in moisture affecting the regions grazed by megaherbivores (see Methods). We compared regional RMACs with deglaciation records as an indicator of the rate and timing of climate-driven environmental changes, and with peatland initiation as a proxy for moisture-driven changes to the landscape (Methods, Supplementary Methods 1, Supplementary References 2–4).

All three proxies are derived from samples distributed over large and heterogeneous geographical regions (Supplementary Methods 1, Supplementary Text 1), providing a broad overview of landscape ecological processes affecting rangeland herbivores at regional scales.

Our dataset reveals that a characteristic pattern, termed the Late Glacial $\delta^{15}\text{N}$ Excursion (LGNE), occurred in every region studied, although not contemporaneously (Supplementary Figs 9–11, 13–16). In North America, Siberia and Europe (inset in Fig. 1a,b,d–f), the RMAC record reveals a period of significantly increased moisture that precedes or accompanies deglaciation and is followed by elevated peatland initiation. The isotope dataset for Alaska's North Slope region ends when horse and bison seem to become locally extinct, but records a rapid rise in moisture leading to this event. Similarly, Patagonian ice sheets limit the age of the South American dataset to <15 kyr BP, but the rapid and marked increase in $\delta^{15}\text{N}$ values after that point indicates a swift change towards decreased moisture levels, suggesting that a moisture spike occurred around the time of ice sheet melting (Fig. 1f). It is apparent that rangelands on all four continents experienced a LGIT moisture spike coinciding with a critical period of extinction and environmental change recorded in pollen, fossil, geological and genetic records (Supplementary Text 1, 5).

Discussion

The persistence of relatively low $\delta^{15}\text{N}$ values (high moisture) through major climate boundaries between warm and cold phases (for example Greenland Stadial 1 to Holocene, Fig. 1c; Antarctic Cold Reversal to Holocene; Fig. 1g) indicates that landscapes remained well supplied with moisture despite changes in temperature (Fig. 2c). The lagged and buffered relationships between temperature, deglaciation and rangeland moisture levels are a consequence of complex input–output dynamics affecting soil moisture, with increased moisture input generating enhanced means of moisture removal (Supplementary Text 1). The RMAC suggests that in each case the final balance of moisture in grazed environments tended towards pre-LGNE levels (Fig. 1a,b,d–f; inset in Fig. 2a–d).

The change in megafaunal ecology detected by the RMAC could reflect either the preferential use of high-quality, ^{15}N -depleted graze that flourishes in well-watered grasslands¹², or the forced adoption of an altered diet driven by moisture-driven environmental change. It seems unlikely that the latter independently drove a similar $\delta^{15}\text{N}$ response in every region, and indeed stable carbon isotopes from the samples (Supplementary Text 2, Supplementary Fig. 12) suggest that the types of plant consumed did not change significantly during the LGNE. This is also consistent with the feeding ecology of the herbivores studied, particularly horses which are obligate grazers. Hence, the RMAC analysis supports preferential grazing of high-quality forage, although this initially seems inconsistent with the displacement or extinction of the grazers, and potentially also the browsers, around the LGIT^{1,3,21,22}. The apparent mismatch between a boon of quality graze and the extinction of mega-grazers around this period has been explained by a 'temporary optimum'¹² or 'transitional period'¹⁶ (Fig. 1c; Fig. 2c). In this model, persistent moisture in deglacial environments altered the selective environment for grasses and forbs (which rapidly produce expendable foliage in response to short-term moisture availability, then survive dry periods as root stocks or seeds) in favour of plants that require more reliable moisture but invest in the production of hardy, herbivore-resistant, perennial foliage^{9,10}. This vegetational turnover is recorded in LGIT pollen records from deglacial environments worldwide^{23–25}, and a key consequence is peatland formation and development, which consistently follows the LGNE in both hemispheres (Fig. 1a,b,d–f). Palaeontological proxies from Eurasia²⁶ and eastern Beringia^{6,22,23} also show a post-LGM spike in the abundance of both steppe vegetation and herbivores, consistent with a short-term boon of quality forage. Thus, the same moisture that provided the boon also appears to have allowed the spread of herbivore-resistant plant communities, probably aided

by a reduction in the facultative consumption of establishing saplings owing to increased graze abundance (Supplementary Text 3).

The moisture–boon–replacement model suggests that the last phase of the LGNE represents a reduction in arid-to-mesic transitional environments as a new balance of rangeland and grazer-resistant biomes is reached (Fig. 2d). The bone $\delta^{15}\text{N}$ data show that graminivores that survived the LGIT (for example bison on the American prairies, horse on Eurasian steppes and llama in South America) all returned to elevated, arid-land $\delta^{15}\text{N}$ values. Meanwhile, where these taxa became extinct (temporarily or permanently) in the far north, mixed feeders (for example caribou, *Rangifer tarandus*, moose, *Alces alces*, and muskox, *Ovibos moschatus*) now dominated, and continued to show comparatively low $\delta^{15}\text{N}$ values¹². Seemingly, therefore, wherever $\delta^{15}\text{N}$ -values remained comparatively low, the rangeland communities declined while mixed feeders/browsers succeeded, as predicted by a moisture-based model of extinctions (Supplementary Text 3 and 4).

The isotopic record therefore suggests that keystone graminivores experienced strong extinction pressure during deglacial and prolonged warming events because the rangeland habitats that they require are particularly sensitive to increasing moisture^{9,10,13,22}. This model can explain why African megafauna experienced a notably lower rate of late Pleistocene extinctions than megafauna on other continents, and why African grazers and their predators were more affected than browsers²⁷. Africa's trans-equatorial position allowed bands of rangeland to persist between the desert and the central monsoon region through the LGIT, despite climate changes that caused the meridional migration of this boundary^{27,28}. The cheetah, a top-level rangeland predator, preserves a genetic record of an extreme population bottleneck around the start of the African Humid Period (~13–5 kyr BP)²⁹, consistent with moisture-associated LGIT contractions in graminivore populations. These may have been less catastrophic than in the Northern Hemisphere, as they were driven largely by increased precipitation rather than meltwater from ice sheets or degrading permafrost. In comparison, the lack of detailed datasets in Sahul (Australia and New Guinea) complicates interpretation, although large-scale moisture changes have been detected in the period around the late Quaternary extinctions³⁰. In both Africa and Sahul, the prospect of using nitrogen stable isotope research to reconstruct moisture patterns offers a new means to improve resolution of the global megafaunal extinction process.

Methods

We compiled new and published dated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements (Supplementary Methods 1 and Supplementary References 1; $\delta^{13}\text{C}$ (‰) = $[(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}}] - 1$). The dataset includes wild horse (*Equus* spp., $n = 340$) and bison (*Bison* spp., $n = 126$) from Europe, Siberia and North America, and camelids (*Lama* spp., $n = 45$) from Patagonia, South America. Additional data from other sources (sediment samples, carnivores, woolly mammoth) were also included in investigations detailed in the Supplementary Information (Supplementary Figs 9–12). The data were grouped into samples of a particular genus within a particular region, and data in each group were Z-transformed to have mean = 0 and s.d. = 1. The RMAC (Supplementary Methods 2 and 3) is constructed based on changes in the central tendency of normalized bison and horse $\delta^{15}\text{N}$ values over time, which are then transformed according to the inverse relationship between $\delta^{15}\text{N}$ and moisture level observed in empirical studies (Supplementary Methods 1 and Supplementary References 5). The RMAC estimates central tendency with a modified kernel smoother designed to respond to changes in average $\delta^{15}\text{N}$ over time more closely where the data are more dense, and to exclude areas where data do not meet reliability requirements. RMACs were generated using 1,000 bootstrap samples of the data, allowing 95th percentile confidence intervals (CI) to be obtained. These were juxtaposed against proxies for temperature, ice sheet extent and peatland initiation from the literature (see Fig. 1 text, Supplementary Methods 1, and Supplementary References 2–4).

Data availability. All isotope data generated or analysed during this study are included in this published article (and its Supplementary Information files). The sources of other proxy data (temperature records, ice sheet extent and peatland initiation) are given in Supplementary References.

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Author contributions

A.C. conceived the project, collected samples and coordinated laboratory work. M.T.R.-W. compiled data from the literature, conceived and implemented analyses, and constructed the figures. All authors contributed to data interpretation. The manuscript was written by M.T.R.-W. and A.C., with input from all authors.

Additional information

Supplementary information is available for this paper.

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Competing interests

The authors declare no competing financial interests.