The large mean body size of mammalian herbivores explains the productivity paradox during the Last Glacial Maximum

Dan Zhu1, Philippe Ciais1, Jinfeng Chang1, Gerhard Krinner2, Shushi Peng3, Nicolas Viovy1, Josep Peñuelas4 and Sergey Zimov5

Large herbivores are a major agent in ecosystems, influencing vegetation structure, and carbon and nutrient flows. During the last glacial period, a mammoth steppe ecosystem prevailed in the unglaciated northern lands, supporting a high diversity and density of megafaunal herbivores. The apparent discrepancy between abundant megafauna and the expected low vegetation productivity under a generally harsher climate with a lower CO2 concentration, termed the productivity paradox, requires large-scale quantitative analysis using process-based ecosystem models. However, most of the current global dynamic vegetation models (DGVMs) lack explicit representation of large herbivores. Here we incorporated a grazing module in a DGVM based on physiological and demographic equations for wild large grazers, taking into account feedbacks of large grazers on vegetation. The model was applied globally for present-day and the Last Glacial Maximum (LGM). The present-day results of potential grazer biomass, combined with an empirical land-use map, infer a reduction in wild grazer biomass by 79–93% owing to anthropogenic land replacement of natural grasslands. For the LGM, we find that the larger mean body size of mammalian herbivores than today is the crucial clue to explain the productivity paradox, due to a more efficient exploitation of grass production by grazers with a large body size.

Mammalian herbivores live in all major terrestrial ecosystems on Earth. During the past decades, our understanding of the important role that large mammalian herbivores (body mass $>10$ kg) have in controlling vegetation structure and carbon and nutrient flows within ecosystems has increased. In herbivore-exclusion experiments, large herbivores have been shown to reduce woody cover, modify the traits and composition of herbaceous species, accelerate nutrient cycling rates, increase grassland primary production, and reduce fire occurrence. In palaeoecological studies, the late Pleistocene megafaunal extinctions have been shown to result in cascading effects on vegetation structure and ecosystem function, including biome shifts from mixed open woodlands to more uniform, closed forests and increased fire activities.

During the last glacial period from 110 to 14 thousand years before present (kyr BP, taken to be AD 1950), the mammoth steppe ecosystem, also referred to as 'steppe–tundra' or 'tundra–steppe', prevailed in Eurasia and North America, covering vast areas that are occupied by boreal forests and tundra today. Characterized by a continental climate, intense aridity and domination of herbaceous vegetation, including graminoids, forbs and sedges, the mammoth steppe sustained a high diversity and probably a high density of megafaunal herbivores, such as woolly mammoths, muskoxen, horses and bison. However, the main driving force behind the maintenance and disappearance of the mammoth steppe remains controversial. Alternative to the climate hypothesis that attributes the end-Pleistocene vegetation transformation and mammalian extinctions to climate change, the 'keystone herbivore' hypothesis argues that megaherbivores have maintained the mammoth steppe through complex interactions with vegetation, soil and climate.

The apparent discrepancy between the late Pleistocene dry and cold climates and the abundant herbivorous fossil fauna found in the mammoth steppe biome has provoked long-standing debates, called the productivity paradox by some palaeontologists. Based on the general relationship that larger animals require less food per unit body weight, a previous study has indicated that higher herbivore biomass densities could be maintained if large species dominate the ungulate community. Studies of modern analogous steppe communities in northeastern Siberia have emphasized the mosaic character of vegetation as a crucial factor in supporting herbivores, with various herbaceous plant types and landscape units of different productivities, depending on local heat and moisture supply that are affected by local topography. However, a large-scale quantitative analysis is missing that analyses how local evidence of abundant megafauna can be reconciled with low vegetation productivity under glacial climates and low atmospheric CO2 concentrations, calling for the integration of interactions between large herbivores and terrestrial productivity within process-based ecosystem models.

Over the past 20 years, dynamic global vegetation models (DGVMs) have been developed and applied to simulate the global distribution of vegetation types, biogeochemical cycles and responses of ecosystems to climate change. However, despite the non-negligible ecological impacts of large herbivores, most of the
current DGVMs, or land surface models that include a dynamic vegetation module, lack explicit representation of large herbivores and their interactions with vegetation. One exception is ref. 30, which included a grazer module in the LPJ-GUESS DGVM and applied it to present-day Africa to study the potential impact of large grazers on African vegetation and fire.11

In this study, aiming to address the productivity paradox, we extended the modelling domain to the globe for two distinct periods: present-day and the Last Glacial Maximum (LGM, around 21 kyr BP), using the ORCHIDEE-MICT DGVM model.32,33 We incorporated the dynamics of large grazers within ORCHIDEE-MICT on the basis of equations that describe grass forage intake and metabolic rates dependent on body size, and demographic parameters that describe the reproduction and mortality rates of large grazers.36,37 (Fig. 1). Feedbacks of large grazers on vegetation were simulated through simplified parameterizations for trampling of trees, grass biomass removal and productivity enhancement by grazing calibrated from field experiments (Fig. 1, see detailed description in the Methods (Effects of grazers on vegetation)). Grazers were represented with a prescribed average body size, whereas browsers (that is, herbivores that eat woody plants) were not included, assuming that herbaceous plants dominated the diet of large herbivores.35,36 Simulated present-day grazer biomass was evaluated against field observations in protected areas across a wide range of ecosystems. For the LGM, we found that the larger mean body size of grazers than today is the key parameter that allows the model to reproduce a substantial density of large grazers on the cold steppe during the LGM.

Results

Present-day grazer biomass. Simulated grazer biomass densities are shown in Fig. 2 for present-day climate conditions. They were in reasonable agreement with the herbivore densities observed in protected areas in ref. 35 (Fig. 2b). Model-data misfits may be due to simplifications of the grazing module (see Methods). First, the lack of browsing processes underestimates food availability for herbivores. This leads to an underestimation of large herbivore populations not only because of missing browsers and underestimated mixed feeders, but also because of underestimated grazers, since conventional grazers can also have some portion of woody plants in their diets, which are affected by available forage types.32,33 Second, the lack of explicit representation of predation, competition for resources, such as water and shelter, poaching in protected areas, outbreak of diseases34 and hunting in the North American ecosystems,35 may lead to an overestimation of large grazer biomass compared to the previously described data.35 In addition, bias of grass productivity in the model can also result in errors in the modelled grazer density. We verified that the simulated global pattern of grass gross primary production (GPP) generally matches an observation-driven dataset36, but that it had an overestimation in subarctic regions (Supplementary Fig. 1). This overestimation of grass GPP might be owing to the high grass fractional cover produced by the vegetation dynamics module (Supplementary Fig. 1a), which does not represent shrubs, mosses and lichens.37

Figure 2a shows the modelled global distribution of potential grazer biomass density for the present-day, after subtracting the fractions of tropical rainforest (see Supplementary Note 1). In order to estimate the reduction in wild large grazers due to human land use, we made use of the anthropogenic biome classification system from the Anthromes v.2 product41, in which land was separated into three major categories: ‘Used’, ‘Seminatural’ and ‘Wild’. We assumed the remnant habitat for large grazers to be the Wild category as a lower estimate, and the Seminatural and Wild categories were used as an upper estimate. The resulting spatial distributions are shown in Supplementary Fig. 2, and the regional total values are listed in Supplementary Table 2.

Simulated global potential biomass of large grazers for the present-day was slightly smaller than the pre-industrial value (Supplementary Table 2), mainly due to a slight decrease in modelled grassland area. This indicates that climate change and the increase of CO₂ by 100 p.p.m. during the past century have had minor effects on potential grazer biomass. However, subtracting the land used by humans led to a 41–83% reduction of the potential biomass of wild grazers for the pre-industrial period, and an even greater reduction (79–93%) for the present-day because of the expansion of agricultural land use and settlements during the past century. Note that the estimated reduction here only considers the direct replacement of wildlife habitats by human land use, whereas other threats to wild grazers, including hunting, competition with livestock, disease transmission from domestic to wild species, loss of genetic diversity and the synergies among these threats, are not included.

LGM grazer biomass. The biomass of large grazers during the LGM is closely related to the vegetation distribution and its productivity. In order to evaluate the simulated LGM vegetation, the plant functional types of the model were regrouped into the mega-biomes of the BIOME 6000 reconstruction based on pollen and plant macrofossil data (Supplementary Note 2). The model can capture the retreat of forests in the northern middle and high latitudes during the LGM, largely replaced by grassland and tundra, in accordance with BIOME 6000 data (Fig. 3a,b). The scarcity of palaeoecological records, however, precludes a more quantitative evaluation of the modelled vegetation distribution.

Figure 3c shows the simulated LGM grazer biomass density for the Northern Hemisphere. The spatial distribution generally matches the distribution of megafaunal fossil occurrences, with 60% of the locations where fossils have been found being in grid cells with a grazer density larger than 500 kg km⁻² (Fig. 3c). Compared with two reconstructions of large herbivore density of around 9 tonne km⁻² in northern Siberia19 and in arctic Alaska31 averaged for the period of 40–10 kyr BP, our simulated grazer density was only about 1 tonne km⁻². This large underestimation is possibly due to: (1) a low bias of our model results using LGM climate, since the reported bone abundance is an average during 40–10 kyr BP30,31, a period during which the LGM corresponds
to the most severe climate; (2) uncertainties in the LGM climate used to force our DGVM model, considering limitations of climate models in capturing sub-continental patterns of temperature and precipitation for the LGM; and (3) the coarse resolution (approximately 30,000 km² for one pixel near 70° N) of our model results that do not capture local conditions of the areas from which the densities were reconstructed (river banks and lowland sections of 10–80 km²). A simple sensitivity test was conducted for the two grid cells corresponding to the previous studies, by setting the temperature to be warmer by 1 or 2 °C and annual rainfall to be higher by 50 or 100% (Supplementary Fig. 3). Grazer biomass density for both grid cells could increase to 4 tonne km⁻² in the case of 2 °C warmer temperature and 100% higher rainfall, indicating a strong sensitivity of grazer biomass to the slightly milder climates in the context of very cold and dry conditions. This strong sensitivity is supported by the evidence of high variations in megafaunal populations during the period of 45–10 kyr BP, with peaks of bone abundance at warm interstadial periods.

**Effects of temperature and body size on grazer biomass density.** Climate conditions control large grazer densities through grass net primary production (NPP), supporting herbivores and the

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**Fig. 2** | Modelled potential large grazer biomass density for the present-day (mean of 1960–2009). **a**, Potential density without consideration of human land use, after subtracting the fractions of tropical rainforest (see Supplementary Note 1). The black crosses symbolize the locations of the empirical data from ref. 37, which are shown in **b** and listed in Supplementary Table 1. **b**, Comparison between empirical herbivore biomass and modelled potential grazer biomass (Pearson correlation coefficient \( r = 0.55 \), \( n = 63 \), \( P < 0.01 \)). The dashed line represents the 1:1 line.

**Fig. 3** | Modelled LGM biome distribution and large grazer biomass density. **a**, Simulated biome distribution at the LGM, converted from the modelled properties of plant functional types (PFTs) using the algorithm described in Supplementary Note 2 (a), and compared to reconstructions based on pollen and plant macrofossil records compiled by the BIOME 6000 project (b). **b**, Adapted from ref. 42, Wiley. **c**, Simulated grazer biomass density at the LGM for Northern Hemisphere (north of 20° N). Blue circles in **c** indicate the dated megafauna fossil localities compiled in a previous study, corresponding to the time interval of 26–20 kyr BP.
In regions with MAT above approximately 0 °C, the grazer biomass-to-grass NPP ratio generally stayed in the range 5–10 (in kg live weight km⁻²; g C m⁻² yr⁻¹; Fig. 4b); whereas in colder regions, the same grass productivity supported a much lower number of grazers, with barely any grazers when MAT is below −10 °C. This strong reduction of grazer biomass per unit of grass NPP under low MATs resulted from: (1) the energy expenditure, which increases exponentially with decreasing temperature for mammals (equation (3)); and (2) the growing season being shorter in high latitude regions compared to tropical and temperate regions, which leads to a longer starvation period with low temperatures, acting to reduce fat reserves and birth rates and to increase starvation-induced mortality (equations (6)–(8)).

Impact of grazing on different taxa, the grazer biomass-to-grass NPP ratios were higher than in the present-day run, especially for colder regions (Fig. 4c, red). The strong reduction in this ratio occurred only below an MAT threshold of approximately −10 °C, instead of 0 °C, as found in the present-day analysis. We further conducted a sensitivity test for the same LGM run, except that A was prescribed as 180 kg ind⁻¹, the same as for present-day in the Northern Hemisphere (see Methods). The relationship between the grazer biomass-to-grass NPP ratio and MAT (Fig. 4c, blue) was mostly similar to that in the present-day analysis, despite larger variations than for the present-day for MATs near 5 °C. Therefore, Fig. 4c shows that a larger body size in the LGM effectively counteracted the effect of colder temperatures on grazer density. As denoted in equations (1) and (3), when body size increases, the maximum forage intake rate increases faster than the energy expenditure, because the scaling exponent of intake in equation (1) (0.88 for grass living biomass and 0.84 for dead grass) is larger than that of energy expenditure (0.75). This leads to a more efficient exploitation of grass production by grazers with a larger body size, thus a higher grazer density supported by the same level of grass production.

The spatial distribution of grazer biomass at the LGM in the sensitivity test with A = 180 kg ind⁻¹ is presented in Supplementary Fig. 6, showing that grazers could have barely existed in the mammoth steppe ecosystem in Eurasia and North America if they had a body mass as low as today’s northern herbivores. The global total grazer biomass would be only 235 million tonnes live weight, much less than that with A = 500 kg ind⁻¹ (319 million tonnes). This suggests that, during the LGM, the cold steppe in the middle and high latitudes was able to sustain substantial quantities of grazers mainly because the mean grazer body size was much larger than today.

**Impacts of grazing on land carbon cycle during the LGM.** Owing to the strong human intervention in today’s biosphere and the human-caused collapse of large herbivore populations, we focus on the LGM to analyse the impacts of grazing on vegetation distribution and the carbon cycle, by comparing the model results with and without grazers. Figure 5 presents the effect of grazers on the global land carbon fluxes during the LGM. Total NPP simulated with...
grazers was 35 Pg C yr\(^{-1}\), 17% higher than without grazers. Turnover times of tree and grass biomass decreased from 12.5 and 0.57 years without grazers to 11.8 and 0.52 years with grazers. For trees, the additional trampling-induced mortality contributes to the faster turnover rate and lower equilibrium biomass than without grazers. For grasses, the continuous consumption by grazers removes aboveground biomass at a higher rate than by normal senescence in the simulation without grazers. For the total vegetation as a whole, turnover rate increased by 31%, not only because of faster cycling in grass and tree biomass, but also because of the smaller total forest area (30 compared to 33 million km\(^2\)). More details on the effect of grazing on tree cover and carbon stocks and fluxes can be found in the Supplementary Discussion.

**Discussion**

We implemented dynamic herbivores and their effects on vegetation types and the land carbon cycle in the ORCHIDEE-MICT DGVM model, on the basis of physiological and demographic equations for large grazers. Evaluation against today’s empirical herbivore biomass data for protected areas across a wide range of ecosystems shows a reasonable model performance in simulating potential grazer biomass sustained by the grassland ecosystems. We then present the global results of potential large grazer biomass for the present-day and the LGM.

In the context of the so-called productivity paradox of the late Pleistocene mammoth steppe biome, our model shows that only if the average body size was much higher than today (500 compared to 180 kg ind.\(^{-1}\)), could high grazer densities be simulated under the harsh climate and low atmospheric CO\(_2\) during the LGM. This property emerges from the different scaling of forage intake and energy expenditure with body size, namely, the allometric exponent of intake (0.88 for living grass and 0.84 for dead grass; equation (1)) is higher than the exponent of expenditure (0.75; equation (3)), the former was obtained from an animal model calibrated for cattle\(^{49}\), and the latter conforms to the metabolic theory\(^{49}\). A collection of body mass and dry matter intake across 46 large mammalian herbivores (body weight > 10 kg)\(^{31}\) gives a value of 0.85 for the scaling exponent (Supplementary Fig. 7), which is indeed higher than the 3/4 power scaling of metabolic rates and production rates\(^{25,29}\), and supports the high values used in our model. Note that the exponent of intake increases with forage digestibility (equation (1)), which are fixed values in the current model. In reality, digestibility varies at different phase of growth, with higher values in the early growing season, and decreases with the accumulating grass biomass\(^{31}\). Therefore, a potential positive feedback of large grazers on forage digestibility is missing from the model. Besides, the scaling exponent was reported to be different between ruminants (around 0.88) and hindgut fermenters (about 0.82)\(^{32}\), thus the value for an ‘average grazer’ may be lower than the values used in the current model, close to the regression coefficient of 0.85 as described in ref. 49.

Evidence from fossil\(^{53,54}\) and extant\(^{55}\) mammal species have shown a long-term trend towards increasing body size in mammals throughout the Cenozoic era, that is, Cope’s rule in evolutionary biology\(^{53}\). This indicates that there are selective advantages for larger body sizes, such as larger guts of herbivores that allow microorganisms to break down low-quality plant materials, and higher tolerance to the cold and starvation\(^{56}\). Our results quantitatively show the importance of body size to explain the productivity paradox, as a larger body size enables grazers to live on the mammoth steppe in substantial densities during the LGM, despite colder temperatures and shorter growing seasons than today. After the end-Pleistocene extinction of species with a large body size, for which the contributions of humans versus fast climate change remaining debated\(^{46}\), the average body size of herbivores reduced, and the boreal and arctic grasslands today can only sustain a low biomass density of grazers (Figs. 2 and 4).

One limitation of our current model is a lack of separation among large herbivore species or types, in particular a specific representation of megaherbivores (body mass > 1,000 kg). The keystone herbivore hypothesis is centred on the pivotal role of
megaherbivores in creating and maintaining an open habitat dominated by fast-growing, more nutritious short grasses and woody plants, the habitat that is crucial for many smaller herbivores. This appears to be supported by observations in present-day Africa, where the white rhinoceros, not the smaller grazers, were able to maintain short grass communities, and where the loss of the white rhinoceros led to declines in smaller grazers such as impala and zebra. This interaction among plants, megaherbivores and smaller herbivores is, however, dependent on vegetation productivity along environmental gradients. Therefore, to expand the ‘average grazer’ in our current model to a framework of herbivore functional types (for example, refs 32,60) is a future priority; and the use of mechanistically coupled herbivore functional types and vegetation dynamics in DGVM models could be a promising tool to quantitatively investigate the ecological impacts of large herbivores.

For the ecological impacts of large grazers, our results show a general reduction in tree cover and an increase in grassland productivity with grazers (Fig. 5 and Supplementary Discussion). The current model, however, does not represent the composition changes of herbaceous species under grazing (which favours annual over perennial plants, short over tall plants, and high over low specific leaf area), as well as competition between shrubs, mosses and grasses under grazing pressure. In a tundra ecosystem, heavy grazing led to a transition from moss-rich heathland to graminoid-dominated steppe-like vegetation, and thus increased aboveground primary production. Therefore, to better simulate grazer-induced changes in the biogeochemical cycle of DGVM models, explicit representation of mosses and shrubs, and their competition with grasses that are affected by grazers, would be required. It is worth noting that to disentangle the relative contribution of these factors, including species changes and increased nutrient availability, to the enhanced productivity is difficult in field-based grazer-exclusion experiments. The lack of a fully closed nutrient cycle in our model also limits its accuracy to estimate the full impact of grazers on ecosystems.

What adds more complexity to the ecological impacts of large grazers is a set of physical properties that are affected by grazing, especially in cold regions. As has previously been argued, during summer, by removing the insulating moss carpet and litter layer, large grazers might increase soil temperature and deepen annual thaw depth and root penetration; during winter, by trampling snow while searching for food, they might lower soil temperature, while quickening the spring melt of snow due to a lower albedo of dirty snow, and therefore lengthen the growing season. To test the magnitude of such effects requires parameterization of these biotic–abiotic interactions in future model developments. Large herbivores may have fundamentally modified the Pleistocene ecosystems; to bring them into large-scale land surface models would help us to better understand the intricate interactions among climate, plants and animals that have shaped the biosphere.

Methods

ORCHIDEE-MICT model overview. ORCHIDEE (Organizing Carbon and Hydrology In Dynamic Ecosystems) is a process-based DGVM model designed for multi-scale applications. It consists of two main modules: SCHEBA for energy and water exchanges and photosynthesis at half-hourly time steps, and STOMATE for vegetation dynamics and the carbon cycle at daily time steps (Fig. 1). The model describes the land surface using a ‘tile’ approach, that is, each grid cell is occupied by a set of plant functional types (PFTs), with the fractional covers of all PFTs adding up to one. In the current model, there are 13 PFTs, including 8 for trees, 2 for natural grasses (C3 and C4), 2 for crops and bare land. PFTs go through the same suite of processes (photosynthesis, phylotaxis, allochton, of carbon assimilates to plant biomass compartments, carbon flow from living biomass to litter pools after senescence and/or mortality, from litter to soil carbon pools, and heterotrophic respiration), but with PFT-specific parameter values, as detailed in ref. 2. The vegetation distribution, that is, the fractional covers of the PFTs, is simulated by the vegetation dynamics module through bioclimatic limits, competition between PFTs for space and light, and a series of mortality processes. The soil thermal and hydrological dynamics are represented by a physically based multi-layer soil structure to simulate heat transfer and water movement between air and deeper soils. These physical processes interact with the vegetation and carbon processes mentioned above (Fig. 1).

Inputs required by ORCHIDEE include meteorological variables (surface air temperature, precipitation, air humidity, incoming short and long wave radiation, wind and air pressure), atmospheric CO2 concentration and soil texture. For each simulation, the model needs to run at first a period of ‘spin-up’, namely, starting from zero carbon fluxes and pools, full cover of bare land, and default values for physical variables, the model gradually approaches an equilibrium state given the inputted climate and atmospheric CO2 conditions. Then, transient simulations for the target time period can be conducted from the last year of spin-up. In ORCHIDEE, the spatial resolution of each simulation depends on the resolution of input climate forcing.

ORCHIDEE-MICT is an evolution of ORCHIDEE with additional high-latitude processes, including a soil-freezing scheme, which simulates the liquid and solid water fractions in the soil and associated energy balance; a multi-layer snow scheme, which improves the representation of snow thermal conductivity and soil temperature, and a vertically resolved litter and soil carbon module considering permafrost processes.

To incorporate grazing processes in ORCHIDEE-MICT, we firstly adapted the structure of ORCHIDEE-GM v.2.1 (grassland management, ref. 2) into ORCHIDEE-MICT, which calculates energy intake and expenditure, reproduction and mortality using empirical relationships with body size. A major difference from the original equations proposed in the model of ref. 2 is that we did not separate animals into age classes, thus there is only one type of average grazer with fixed mature body mass (denoted as A). Detailed implementations are described below.

The grazer population model. Daily intake and expenditure. For wild large grazers, the reduction in food resources during the non-growing season critically limits their density. Unlike domestic livestock on pastures that can be fed on forage grass or crop products, wild herbivores resort to various ways to acquire energy during the non-growing season, such as migration and feeding on dead grasses. In the grazing module in ORCHIDEE-MICT, in order to sustain grazers throughout the year, especially for the high-latitude regions with a short growing season, we divided the simulated aboveground litter pool of grass PFTs into two parts, an edible pool (Led, representing plant residues) and an inedible one (representing animal excreta) (Fig. 1). Grazers are allowed to eat Led, when confronted with insufficient AGB (aboveground grass biomass of three tissues represented in ORCHIDEE, that is, leaf, sapwood and fruit).

Maximum daily intake. The maximum forage intake in units of energy is related to grazers’ body size and forage digestibility (d), since a low digestibility diet decreases the rate of digestion of ungulates and thus limits the maximum intake, which is calculated as in the previously described model:

\[ I_{\text{DM,max}} = 0.334A^{0.57}A_{B}^{0.077}d^{1.73} \]

Maximum daily intake in units of dry mass (DM) is converted from \( I_{\text{DM,max}} \) by:

\[ I_{\text{DM,max}} = \frac{I_{\text{DM,max}}}{ME \times DE} \]

where \( I_{\text{DM,max}} \) (kg DM d\(^{-1}\) ind.\(^{-1}\)) is the maximum daily net energy intake per individual; \( A \) (kg live weight ind.\(^{-1}\)) the mean grazer body mass; \( d \) the forage digestibility, fixed at 0.7 for AGB and 0.4 for Led, following ref. 2. Daily energy expenditure. Energy expenditure in the model is applied to tropical grasslands was a function of body mass only, and did not account for environmental conditions. Ambient temperature has been shown to significantly affect energy expenditure for endotherms. Because we aimed to apply the model globally, we introduce the following equation to account for temperature-dependent metabolic rate:

\[ E = E_0 \times \left( \frac{T}{T_0} \right)^{4/3} \]

where \( E_0 \) (MJ kg\(^{-1}\) d\(^{-1}\) ind.\(^{-1}\)) is the basal metabolic energy content, calculated as 15.6 \times d, following ref. 2; and \( d \) is the digestible energy proportion in the forage not excreted in the faeces, fixed as 50%.
where $E$ (MJ d$^{-1}$ ind.$^{-1}$) is the daily energy expenditure per individual; $T$ ($^\circ$C) the long-term mean air temperature for each grid cell, calculated in the model using a linear relaxation method (see equation 3 in ref. 32) with an integration time of three years; $k_s = 0.0079$, derived from the regression model of ref. 50; $b_s = 0.125$, calibrated to yield a range close to the values in ref. 34. Note that this parameterization may overestimate energy expenditure for large herbivores that are adapted to cold climates, such as woolly mammoths and muskoxen, which may spend less energy owing to their insulating heavy hair coat and thick fat layer.

Conversion between energy and fat storage. Fat is the main energy reserve and affects the survival of grazers confronted with food shortages31. The daily change in fat storage is calculated as:

$$ \frac{dF}{dt} = \frac{I - E}{m \times (E_{\max} - F) + E} $$

where $F$ (kg ind.$^{-1}$) is the fat mass per animal, $I$ (MJ d$^{-1}$ ind.$^{-1}$) the actual daily net energy intake (described below); $m$ (kg $^{-1}$) the conversion coefficient between energy and fat, set to 39.3 if $I < E$ (catabolism) or 54.6 if $I > E$ (anabolism) (ref. 34). Note that the body mass, $A$, is a fixed parameter in the model, neglecting the daily changing $F$.

Actual daily intake. The actual daily intake depends on the amount of available foraging material. At each daily time step, the model determines whether grazers feed on AGB, $L_{\text{agb}}$, or nothing, by comparing the daily forage requirement, calculated as $P \times \text{AGB} \times X_P$, given a population density $P$ (ind. km$^{-2}$) calculated by the model (see below), with the amount of available AGB or $L_{\text{agb}}$. Grazers are assumed to feed in priority on (1) AGB, if available AGB exceeds the AGB requirement; (2) $L_{\text{agb}}$, if condition (1) is not met and $L_{\text{agb}}$ exceeds the $L_{\text{req}}$ requirement; and (3) nothing, if neither conditions (1) nor (2) are met. Note that $L_{\text{agb}}$ for AGB is higher than for $L_{\text{agb}}$, that is, the AGB requirement is always higher than the $L_{\text{req}}$ requirement, according to equation (1) and (2). A buffer of five days is set to prevent grass from being grazed at the beginning of the growing season, that is, the grazers are assumed to wait for five days to eat AGB after it first exceeds the forage requirement.

Actual intake also has a constraint so that a maximum fat storage cannot be exceeded, which is given by:

$$ I = \begin{cases} L_{\text{max}} & \text{if } I + \frac{E}{m} \leq L_{\text{thresh}} \\ m \times (E_{\max} - F) + E & \text{otherwise} \end{cases} $$

where $E_{\max}$ (kg ind.$^{-1}$) is the maximum fat mass, set to 0.3 $\times$ $A$ (ref. 34). Note that the reduction factor of $L_{\text{agb}}$ with decreasing vegetation biomass density in the original model 1 is not used here, assuming that the grazers have good access to the foragable material and can fulfil their daily demand whenever AGB or $L_{\text{agb}}$ is higher than the forage requirement.

Grazer population dynamics. In ORCHIDEE-MICT, the grazer population density is updated at the end of each year, based on calculated annual mean birth and mortality rates, as described below.

Birth rate. The birth rate depends on body condition, represented by a function of the ratio of the fat storage to the maximum fat mass, following ref. 32:

$$ B_{\max} = \frac{0.8}{1 + e^{-1.5 \times \left( \frac{L_{\text{max}}}{L_{\text{max}}} - 1 \right)}} $$

where $B_{\max}$ (yr$^{-1}$) is the maximum birth rate, calculated at a daily time step and averaged over the year to be used in equation (7).

In this study, the actual birth rate is also constrained by fat storage, which implicitly considers the energy investment in breeding:

$$ B = \min \left( B_{\max}, \frac{m \times X_P}{F_{\text{365}}} \right) $$

where $B$ (yr$^{-1}$) is the actual birth rate at the end of the year. Then the amount of energy $\frac{8 \times X_P}{365}$ is subtracted from $F$ to account for the energy transferred to newly added grazers.

Mortality rate. In the previous model 1, mortality was caused by the exhaustion of fat storage during periods of food shortage. In ORCHIDEE-MICT, we define it as starvation-induced mortality ($M_s$) and calculate it using the same method as in the previous model 1: we assume the fat storage to be a normal distribution with a mean $\mu = F$ and a standard deviation $\sigma = 0.125 \times F_{\text{max}}$; then the cumulative distribution function of fat storage returns the probability (defining the value for $M_s$) that fat mass is below a prescribed threshold $F_{\text{max}}$. The value of $F_{\text{max}}$ was set to 0 in the previous model 1, but we set $F_{\text{max}}$ at 0.2$\times$ $F_{\text{max}}$, so that the grazers, especially those on temperate and boreal grasslands, could tolerate longer periods of starvation. The mortality rate $M_s$ in the unit of yr$^{-1}$ is calculated at daily time step and averaged over the year.

In addition to $M_s$, two other causes of mortality are taken into account: (1) a background mortality rate ($M_b$), which is defined as the inverse of animal lifespan, fixed at 25 years 1, and (2) a density-dependent mortality rate ($M_d = k_a \times P$), which represents the fact that a higher density leads to a more intense competition between animals for limited resources (for example, water and living space) and to more frequent epizooic diseases.

Therefore, the equation to calculate the annual density increase of grazer population density is:

$$ \frac{dP}{dt} = B \times P - M_s \times P - M_b \times P - M_a \times P^2 $$

where $P$ (ind. km$^{-2}$) is the grazer population density, updated each year; $P$ is initialized as $P_0 = 0.001$ ind. km$^{-2}$; whenever $P$ is below $P_0$, $P$ is reset to $P_0$ and $F$ is reset to $0$. $k_a$ is the slope of the density-dependent mortality function, calibrated based on the property of equation (5) that the maximum $P$ equals to $\frac{b}{d}$ given an infinite time under constant optimal condition ($M_s = 0$, $M_b = 0.04$, and $b = 0.6$ according to equations (6) and (7)); the value of $k_a$ is therefore set to $\frac{1}{\text{ind. km}^{-2}}$ derived from observed maximum densities of approximately 15–18 $\times$ 10$^3$ ind. km$^{-2}$ for large herbivore biomass observed in protected areas across Africa today (ref. 7, Supplementary Table 1).

Effects of grazers on vegetation. A direct negative impact of grazers on grass productivity is through biomass removal by grazing. This is included in the coupling between grazing and carbon cycle processes, as leaf area index (LAI) is updated every 10 days and reduced after the leaf area loss. In addition, a positive effect on grass productivity due to regrowth after defoliation is represented in the model by, first, the leaf age-related photosynthetic capacities, with younger leaves having a higher photosynthetic efficiency (see equation A12 in ref. 1) and, second, the leaf age-related specific leaf area (SLA), with younger leaves having a higher SLA and subsequently a more rapid increase in LAI during the daily grazing event than if SLA was constant. Grazers could also positively affect grass productivity through accelerating nutrient turnover and modifying the traits and composition of herbaceous species 34,35, which may be more important than the regrowth effect. To explicitly represent these effects is difficult, partly because our model lacks an explicit nutrient cycle and has limited herbaceous plant functional types (only two grass PFTs, C3 and C4, for natural non-woody plants) with fixed sets of traits, partly because the observed enhancement of grass production by grazing in field experiments is a result of various effects mentioned above, making it difficult to be used for calibrating parameters for each individual pathway in a model. Therefore, we used a simple parameterization, that is, a grazer density-related photosynthetic capacity, to coarsely approximate the positive effects of grazers that are associated with accelerated nutrient cycling and changes in traits and/or composition, as described below.

Grazer density-related $v_{\text{max}}$ and $j_{\text{max}}$. The enhancement of primary production by grazing has been observed in a wide range of ecosystems, such as African savannas 36, South American grasslands, and Arctic tundra 37,38, in a tree-population dynamics model developed for the Serengeti–Mara woodlands 37, a value of 7% yr$^{-1}$ was proposed for tree mortality caused by elephants, when the elephant biomass density was around 2,000 kg km$^{-2}$, which accounted for 25% of the total herbivore biomass in that region 37. This grazer-induced tree mortality is higher than the simulated tree mortality in tropical forests by ORCHIDEE-MICT of about 3% yr$^{-1}$. Because the current version of ORCHIDEE-MICT lacks a specific shrub PFT, we introduced a grazer trampling-related mortality only for the tree PFTs, defined as a linear function of grazer population density:

$$ v_{\text{max}} = v_{\text{max}}^0 \times (1 + k_s \times \text{ind. km}^{-2}) $$

where $k_s = 1$, that is, a maximum twofold increase from animal-induced nutrient availability, qualitatively in agreement with the results of grassland fertilization experiments compiled in ref. 39 giving a response ratio of approximately 1.7–2 (primary production in grassland manipulative experiments with nitrogen and phosphorus addition divided by the value in control treatments). The parameter $k_s$ is set to 10$^3$, calibrated on the basis of the observed response of aboveground NPP to herbivores of ref. 39.
where $M_{\text{tress,plant}}$ is the grazing-induced mortality rate of tree PFTs each day ($d^{-1}$); $k_{\text{tress,plant}}$ is set to 2.4 x 10$^8$ d$^{-1}$, in order to match the observed elephant-induced tree mortality of ref. 41.

Evaluation data. Empirical present-day herbivore data. To evaluate the model, we compared the simulated present-day grazer density with the empirical data for large wild mammalian herbivores across various ecosystems (with low human footprints) that has previously been compiled42. Because the focus of the previous study23 was on predator–prey relationships and excluded megaherbivores, such as elephants and rhinoceros, we re-calculated the total herbivore biomass density for each community, including all reported herbivore species from the raw data obtained from ref. 23. Multi-year data for the same ecosystem were averaged, giving 23 protected areas in Africa, 25 in Asia, and 15 ecosystems in North America (Supplementary Table 1). Note that the 15 ecosystems in North America are not game reserves, and human hunting probably decreases animal densities below the local carrying capacities. The empirical herbivore biomass data included both grazers and browsers, whereas our model could only simulate grazer densities. In the model–data comparison, it was thus assumed that grazers dominated the herbivore species23, which may be ecosystem-specific.

Reconstruction data for palaeomegafauna. Few studies have investigated the megafaunal populations present in biomes in the mammoth steps during the late Pleistocene epoch. By analysing C3-dated animal bones accumulated in forest loess in Siberia and Alaska, a previous study estimated an average herbivore biomass of $10$ tonnes km$^{-2}$ over the period of $40$–$10$ kyr BP in northern Siberia, and another study estimated a similar value of $9$ tonnes km$^{-2}$ for the same period in arctic Alaska. Although the bone abundance varied markedly with time, suggesting temporal instability of the mammoth steps during the $30,000$-year period, these estimates are the best available to date providing information on the magnitude of the biomass of large herbivores at the LGM for comparisons with the simulations. The geographical ranges of ice-age megafaunal species are useful indicators of their presence in a grid point of the model. A previous study compiled a dataset of approximately $800$ dated megafaunal fossil localities spanning the past $50,000$ years. As a compromise between the number of localities and the period that could be considered coeval to the LGM, we selected the time interval of $26.5$–$20$ kyr BP of these fossil localities (in total $215$ localities) to compare with our results at the LGM. Note that debate still exists regarding the chronological definition of LGM (for example, ref. 23), and that northern ice sheets peaked before $25$ kyr BP. Overlaying the fossil localities onto the simulated herbivore biomass density of large grazers enables a qualitative evaluation of the model results, although the incomplete list of fossil localities may under-represent the megafauna’s actual distribution ranges23.

Model setup. Global runs with ORCHIDEE-MICT for the present-day and LGM were conducted, as described below and summarized in Supplementary Table 3.

Present-day. For the present-day analysis, ORCHIDEE-MICT was forced by the six-hourly CRU-NCEP gridded climate dataset at 2° spatial resolution (https://vesg.ipsl.upmc.fr/thredds/fileServer/p529/nov/cruncep/readme.html). The model was first run for a 200-year spin-up to reach equilibrium for vegetation biomass and grazers for the pre-industrial period, by repeating the CRU-NCEP 1901–1910 climate data (owing to a lack of gridded climate data for the pre-industrial period) and constant pre-industrial CO$_2$ concentration (285 p.p.m.). Then a transient simulation for 1860–2010 was started from the last year of the spin-up, forced by CRU-NCEP reanalysis data from 1901 to 2010 (for 1860–1900, CRU-NCEP 1901–1910 climate were cycled) and by rising CO$_2$ concentrations. The model results for grazer biomass density averaged from 1960 to 2009 were used as present-day, which roughly corresponded to the period for the data compiled in ref. 23. Because grazers in the model only appear on the grass fraction of the land, grazer biomass density for the entire grid cell was therefore calculated using the following equations:

$$G_b = P_{G} x A x V_{GC} + P_{C} x A x V_{CC}$$

where $G_b$ (kg km$^{-2}$) is the grazer biomass density for grid cell i; $P_{G}$ and $P_{C}$ (ind km$^{-2}$) are the respective grazer population densities for the two types of grass PFTs, C3 and C4; and $V_{GC}$ and $V_{CC}$ are the fractional cover of the two grass PFTs. The grazer body size, $A$, is a key parameter in the model. Note that the value of $A$, in the concept of the average grazer in our current model, is the abundance-weighted average body size over different species, that is, the total animal biomass divided by total animal population. For the present day, because the provided the population of each herbivore species, a mean body size of around 300 kg across 23 ecosystems in Africa and of around 180 kg across the ecosystems in both Asia and North America was derived. Therefore, we fixed $A$ at 300 kg ind$^{-1}$ for Africa and 180 kg ind$^{-1}$ for the rest of the world in the present-day run. Only natural PFTs were simulated in all runs, excluding agricultural land cover.

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References

1. Ripple, W. J. et al. Collapse of the world’s largest herbivores. Sci. Adv. 1, e1400103 (2015).
2. Sandom, C., Faurby, S., Sandel, B. & Svenning, J.-C. Global late Quaternary megafauna extinctions linked to humans, not climate change. Proc. R. Soc. B 281, 20133254 (2014).
3. Anser, P. C., Wood, T. S., Al allergy, S. R., et al. Large-scale impacts of herbivores on the structural diversity of African savannas. Proc. Natl Acad. Sci. USA 106, 4947–4952 (2009).
4. Olofsson, J. et al. Herbivores inhibit climate-driven shrub expansion on the tundra. Glob. Change Biol. 15, 2681–2693 (2009).
5. Diaz, S., Noy–meir, I. & Cabido, M. Can grazing of herbaceous plants be predicted response from simple vegetative traits? J. Appl. Ecol. 38, 497–508 (2001).
6. Diaz, S. et al. Plant trait responses to grazing? A global synthesis. Glob. Change Biol. 13, 313–347 (2007).
7. Frank, D. A., Groffman, P. M., Evans, R. D. & Tracy, B. F. Upland stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. Oecologia 123, 116–121 (2000).
8. Olofsson, J., Stark, S. & Oksanen, L. Reindeer influence on ecosystem processes in the tundra. Oikos 2, 386–396 (2004).
9. Frank, D. A. & McNaughton, S. J. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96, 157–161 (1993).
10. Fulk, J. S., Schmidt, N. M., Christensen, T. R. & Ström, L. Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high Arctic mire. Environ. Res. Lett. 10, 045001 (2015).
11. Sinclair, A. R. E. et al. Long-term ecosystem dynamics in the Serengeti: lessons for conservation. Conserv. Biol. 21, 580–590 (2007).
12. Gill, J. L. Ecolocial impacts of the late Quaternary megaherbivore extinctions. New Phytol. 201, 1163–1169 (2014).
74. Eggleston, H. S. et al. (eds) 2006 IPCC Guidelines for National Greenhouse Gas Inventories (IGES, Kanagawa, 2006).
75. McNaughton, S. J., Ruess, R. W. & Seagle, S. W. Large mammals and process dynamics in African ecosystem. *Bioscience* 38, 794–800 (1988).
76. McNaughton, S. J. Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* 55, 259–294 (1985).
77. Frank, D. A. & McNaughton, S. J. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* 73, 2043–2058 (1992).
78. Elser, J. J. et al. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10, 1135–1142 (2007).
79. Caughley, G. The elephant problem—an alternative hypothesis. *Afr. J. Ecol.* 14, 265–283 (1976).
80. Dublin, H. T. *Decline of the Mara Woodlands: The Role of Fire and Elephants*. PhD thesis, Univ. British Columbia (1986).
81. Väisänen, M. et al. Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nat. Clim. Change* 4, 384–388 (2014).
82. Dublin, H. T., Sinclair, A. R. E. & McGlade, J. Elephants and fire as causes of multiple stable states in the Serengeti–Mara Woodlands. *J. Anim. Ecol.* 59, 1147–1164 (1990).
83. Clark, P. U. et al. The Last Glacial Maximum. *Science* 325, 710–714 (2009).
84. Hughes, P. D. & Gibbard, P. L. A stratigraphical basis for the Last Glacial Maximum (LGM). *Quat. Int.* 383, 174–185 (2015).
85. Monnin, E. et al. Atmospheric CO₂ concentrations over the last glacial termination. *Science* 291, 112–114 (2001).

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**Author contributions**
D.Z. and P.C. designed the study. D.Z. led the writing and performed the analysis, with critical input from P.C. and G.K. J.C. contributed to the model development. S.P., N.V., J.P. and S.Z. enriched the discussion of the results.

**Competing interests**
The authors declare no competing interests.

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   The ORCHIDEE-MICT land surface model is written in Fortran 95. Scripts to analyze model outputs and to plot the figures are written in python.

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