TITLE: PLEISTOCENE ARCTIC MEGAFAUNAL ECOLOGICAL ENGINEERING AS A NATURAL CLIMATE SOLUTION?

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Abstract

Natural Climate Solutions (*NCS*) in the Arctic hold the potential to be implemented at a scale able to substantially affect global climate. The strong feedbacks between carbon-rich permafrost, climate, and herbivory suggest an *NCS* consisting of reverting the current wet/moist moss & shrub-dominated tundra and the sparse forest-tundra ecotone to grassland through a guild of large herbivores. Grassland-dominated systems might delay permafrost thaw and reduce carbon emissions –especially in Yedoma regions, while increasing carbon capture through increased productivity and grass and forb deep root systems. Here we review the environmental context of megafaunal ecological engineering in the Arctic; explore the mechanisms through which it can help mitigate climate change; and estimate its potential – based on bison and horse, with the aim of evaluating the feasibility of generating an ecosystem shift that is economically viable in terms of carbon benefits and of sufficient scale to play a significant role in global climate change mitigation. Assuming a megafaunal-driven ecosystem shift, we find support for a megafauna-based arctic *NCS* yielding substantial income in carbon markets. However, scaling up such projects to have a significant effect on global climate is challenging given the large number of animals required over a short period of time. A first-cut business plan is presented based on practical information –costs and infrastructure– from Pleistocene Park (north-eastern Yakutia, Russia). A 10-yr experimental phase incorporating 3 separate introductions of herds of ~1,000 individuals each is costed at US$114 million, with potential returns of ~0.3-0.4% yr^{-1} towards the end of the period, and >1% yr^{-1} after it. Institutional friction and the potential role of new technologies in the reintroductions are discussed.

1. Introduction

Rapid climate change [1] and biodiversity decline [2] pose huge challenges to humankind and call for new approaches involving active nature management strategies that are able to secure the resilience of ecosystems. In this context, there is a growing interest in the potential of Nature-based Solutions, defined by the IUCN as "*actions to protect, sustainably manage, and restore natural or modified ecosystems, that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits*". The 2015 Paris Agreement on Climate Change signified a high-level recognition of the potential for natural ecosystems to play a role in tackling climate change: 66% of signatories committed to Nature-based Solutions in their climate pledges. Natural Climate Solutions (*NCS*) involve improved land management and ecological restoration practices that avoid emissions and/or increase carbon sequestration. Griscom *et al.* [3] estimated that in the next 20 years *NCS* could contribute over a third of the CO_2 mitigation to keep the planet on a 2ºC pathway. The emerging *NCS* narrative particularly emphasises forests as carbon sinks, but there is increasing interest to expand the focus to climate solutions in non-tree ecosystems including peatlands, grasslands and agriculture [4].

Concurrent with these developments in climate policy is the rise of a new paradigm of recovery-based conservation and environmental management under the label of rewilding. Rewilding [5] is an approach to ecological restoration that aims to restore trophic complexity, stochastic disturbance events, and the ability of organisms to disperse over time and space. The degree to which each can be achieved is dependent on context, vision and ambition [6]. On the spectrum of rewilding initiatives, one of the boldest is the restoration of ecosystems and ecosystem functions which were at least partly or fully lost due to the megafaunal late-Pleistocene/early-Holocene (*LP/EH*) extinctions [7]. The science and practice of rewilding has emerged in different contexts, but can be understood as a response to new insights on: *i)* the co-evolution of grassland systems with grazing and browsing herbivores and the role of megafauna in creating and modifying both biotic and abiotic habitat components [8-10]; *ii)* the large-scale modification of Earth System processes brought about by the megafaunal extinctions in *LP/EH*, encompassing fire regimes, community composition [11], biogeochemical cycling [9, 12, 13], hydrology [14], and the global climate [15]; *iii)* a new emphasis on restoring ecosystem process and dynamics and the role of these in generating diversity, abundance and resilience [16]; *iv)* a desire for wilder natures and a more hopeful and empowering environmental narrative [17]. In Europe, rewilding practice is inspiring the creation of new natural assets that 'take inspiration from the past' but are designed to generate nature-based solutions to a range of social and environmental challenges, including climate change [18].

Rewilding initiatives have generally targeted areas and ecosystems with missing functional species and where wildlife populations and trophic complexity has been downgraded by human practices. A distinctive feature of rewilding is that it responds to new knowledge on the ecosystem impacts of past large-bodied faunal extinctions [19, 20]. The potential for trophic rewilding in the Arctic has become an increasing focus of discussion [21]. Since rewilding is usually associated with restoring degraded ecosystems, Arctic rewilding (and more particularly Pleistocene Arctic Rewilding) requires some explanation and assumptions, given that this biome is often seen as free of high-intensity human disturbance and hence *natural* or *wild*. Ample evidence exists on *i)* the current effects of large herbivores on the resilience of treeless tundra against the encroachment of erect woody plants [22] and on the resilience of grasslands against moss- and shrub-dominated tundra [23]; and *ii)* the role of human expansion across the high latitudes in the *LP/EH* extinction of key megafauna species [24]. Whereas *(i)* links large animals to key properties such as carbon sequestration, productivity, albedo, the hydrological cycle, and the energy budget of the Earth surface (including the dynamics of the upper layers of the permafrost), *(ii)* questions the degree of natural intactness of tundra ecosystems and justifies considering rewilding strategies in the terrestrial Arctic. In this study we will refer to *Pleistocene Arctic rewilding* as a form of *Megafaunal Ecological Engineering* (MEE), because the inherent *restoration* component embedded in the term *rewilding* would require considering the Arctic tundra a degraded ecosystem.

The characteristics of the terrestrial Arctic –loosely defined in here as the high latitude regions covered by tundra and forest-tundra and underlain by permafrost, **Fig. 1**– make it singular in terms of opportunities and challenges for *MEE*. Low human population densities (but by no means lack of people or of millennia-long land use) and remoteness from large urbanised and industrial centres; extreme abiotic conditions (notably the high seasonality in light and temperature and the pervasive role of ice and snow) that have prevented the development of agriculture; fast rates of warming (0.76ºC/decade over 1998-2012; > 6x Earth's average [25]); provide an opportunity, and perhaps and imperative, to test whether *MEE* can create more resilient/adaptable ecosystems. Further, in the Arctic such actions can be conceived at a scale that can influence the functioning of the Earth System globally on its own through carbon cycle and energy balance modification, most notably –but not only– if the large amounts of carbon stored in its deep permafrost soils are accounted for. It is thus timely to assess the feasibility of one of the most audacious hypotheses proposed in this region [14, 26], namely that reconstituting an arctic large-herbivore guild at sufficient density will stabilise the permafrost-climate warming positive feedback [27].

In this paper, we present an initial assessment of whether megafaunal ecological engineering at a large scale (i.e. that able to modify the global carbon and climate systems) is within the bounds of the possible. Such an action would require megafaunal engineering at a scale not previously considered. We do so by *i)* reviewing the environmental context of *MEE* in the Arctic; *ii)* exploring the mechanisms through which *MEE* can help fight climate change; and *iii)* analysing the potential and practicalities of such initiatives at scales where they could make a significant contribution to climate mitigation and adaptation. As an example, we draw on Pleistocene Park in north-eastern Siberia. If successful, such an initiative may constitute a first-order *NCS* form of geoengineering.

2. Arctic Terrestrial Ecosystems: effects of defaunation and trophic downgrading

Pollen, plant macrofossils, and ancient DNA (aDNA) suggest that during the Quaternary, ice-free Northern Hemisphere terrestrial environments north of 40ºN were largely dominated by open landscapes that formed a grassland biome, referred to as the *mammoth steppe,* that sustained a guild of large herbivores including mammoth, woolly rhino, bison, horse, elk and reindeer [26]. Such a biome was not a uniform grass carpet, but instead a savanna-like mosaic, with trees and shrubs on poor soils and productive grasslands on loess and loamy soils [26]. Heterogeneity of plant functional types was probably topography-mediated [28], for example through soil moisture [29]. The abundance of predators (wolf, cave lion) [26] also contributed to the heterogeneity of vegetation cover through the generation of landscapes of fear [30]. But how stable was this system, and how long did it last under different climatic conditions?

The identification of this biome in the fossil record is not straightforward. Fossil pollen-based reconstructions struggle to identify steppe and dry tundra, since it is partly defined by the presence of grass species [31] that cannot be identified below the family level [Poaceae; 32]. Further, pollen is thought to be rare in heavily grazed grassland since there is much vegetative reproduction [26]. Macrofossil findings add clearer taxonomical information, but are rarer [29]. A precise quantification of the dominance of steppe *vs.* tundra in the Arctic in the late Quaternary is thus challenging. Notable insights have come from environmental aDNA [33], despite the still incomplete reference libraries of mammoth steppe species upon which these studies depend. Willerslev *et al.* [33] targeted the mammoth steppe in their pan-Arctic aDNA study of the last 50ka, using a limited library of mammoth steppe plant taxa, plus nematode indicator species. Their study clearly shows that mammoth steppe dominated the Arctic landscape for much of this period. The suggestion that the mammoth steppe was dominated by forbs –with graminoids amounting to <20%– in contrast to pollen-based reconstructions [33] requires further research. The technique used in [33] favours the amplification of forb DNA [34] and the likely over-representation of forbs in soil DNA [35], although especial attention was paid to include as many graminoids as possible in [33]. Beyond 50ka, previous interglacials were likely characterised by more open vegetation than the Holocene [30, 36].

A major ecological shift occurred in the *LP/EH*. The vast herds of large herbivores collapsed as humans moved into the area [24, 26, 37, 38]. Wet and shrubby present tundra established in much of the terrestrial vegetated Arctic, with larch forest dominating the permafrost regions of north-eastern-Eurasia [26]. Wetter soil conditions are inferred from increases in peatland, lakes, and *Sphagnum* fossil pollen after 14ka cal BP [31], as well as in sedimentary aDNA of aquatic taxa [33]. Nematode species employed as indicators of steppe *vs.* tundra show a dominance of steppe indicators before and during the Last Glacial Maximum (*LGM*), with tundra nematodes dominating after 10 ka cal BP [33]. Evidence thus suggests that the Holocene in the Arctic and high latitudes of the Northern Hemisphere is non-analogous to the late Pleistocene, even when compared with previous interglacials [36]: its flora is different [33], as are its soils, and the guild of large megaherbivores is gone.

An important question with regards to Arctic *MEE* is to which extent the mammoth steppe was generated and controlled by large herbivore herds. Zimov *et al.* [14, 26] maintain that the mammoth steppe was “created and maintained” by these animals. Several mechanisms have been identified to drive this top-down control, such as increased nutrient cycling, selection in favour of more palatable species, increased evapotranspiration associated with the dominance of grasses and forbs, together with the bark-stripping behaviour of many mega-herbivores such as bison [14, 30]. Current experimental evidence from herbivore enclosures confirms these mechanisms [21, 30], and it is likely that such effects would be even more remarkable than current observations with extant fauna in the presence of the extinct megafauna [30]. Further evidence comes from the fossil record: herbivory represented a significant vegetation driver on glacial-interglacial cycles in north-eastern Siberia during the Pliocene and early Pleistocene, potentially decoupling it from climate forcing [39]. This does not mean that the mammoth steppe was static: it was a likely highly dynamic biological system that offered higher resilience to external forcing given its very intense biotic component. Finally, *i)* the facts that the inferred mammoth steppe climatic niche is within the current climatic envelope of northern Siberia, Alaska, and Yukon, and *ii)* the state of the Arctic Holocene as a moist/wet tundra-dominated interglacial [26] further agree with the hypothesis that the megafaunal extinctions of the *LP/EH* radically modified land cover and soil conditions in these regions, and that current terrestrial Arctic ecosystems might indeed be heavily affected by the 'ghosts of nature's past' [40].

Despite not all Arctic megafauna going extinct at the *LP/EH*, the mammoth steppe has not developed during the Holocene [except for small refugia; e.g. 41], even in North America where the bison, but not the horse, survived. This would give weight to the *climate hypothesis* for ecosystem change following the *LP/EH* [e.g. 42]. However, Holocene diversity of herbivores (and thus dietary diversity) was much lower than during the Pleistocene, and most importantly, human hunter-gatherer societies have been present in the high latitudes of Eurasia and America throughout, adding pressure on species which have long generation times and slow growth rates, and thus probably keeping them at low densities [43]. No estimates of megaherbivore density in the Holocene come close to those estimated for the Pleistocene mammoth steppe [26].

Independently of what caused the Arctic megafaunal extinctions, the likely large consequences of the megaherbivore extinctions for terrestrial Arctic ecosystem dynamics set the stage for Arctic *MEE*. van der Wal [23] argues that large herbivores are able to change the state of vegetated Arctic terrestrial ecosystems by increasing their carrying capacity through favouring more productive grasslands through the mechanisms discussed above. Hence, the reintroduction of large herbivores in large enough densities might favour a phase transition in regions where climatic conditions could allow alternative vegetation states [30]: such regions have been estimated to cover ~ 42% of the vegetated Arctic [23]. The role of herbivory in decoupling vegetation from climatic conditions –both seen in present experiments [21, 44] and in the palaeoecological record [39]– strongly suggests that it could confer increased resilience to Arctic terrestrial ecosystems to changes in climate.

3. Arctic lands and the global carbon budget

The climatic oscillations of the Quaternary implied large changes in ice sheet, sea ice, and ice shelf extents in the Arctic [45]. Although their spatiotemporal dynamics are not yet fully resolved, especially for periods prior to the *LGM*, large parts of the high latitudes in the Northern Hemisphere have lacked land ice over several glacial/interglacial cycles, despite very low temperatures that promoted the existence and expansion of permafrost. In particular, low moisture during the late Pliocene and Pleistocene meant that the region stretching from eastern Siberia to Alaska (broadly corresponding to the area known as Beringia) remained largely free of glacial ice and its scarifying effects [46]. A thick (up to 50m) sedimentary layer of fine-grained, ice-rich, aeolian-deposited sediment accumulated since Marine Isotope Stage (MIS) 4 (71-60 thousand years ago) in the oldest places and ended abruptly at the Pleistocene/Holocene transition [47]. This layer includes large amounts of fossil material and organic matter, preserved in deep permafrost and known as Yedoma in Russia [48]. The Holocene development of peatlands has given rise to another, younger large high latitude carbon reservoir [49] (**Fig. 1**). The possibility that such large quantities of permafrost-stored carbon become vulnerable due to rising temperatures and permafrost thaw –especially abrupt thaw in ice-rich regions [50]– is one of the main positive climate feedbacks identified in the large latitudes [51]. Lenton *et al.* [52] suggest that such an Arctic permafrost tipping point is already “active”.

The terrestrial permafrost regions of the Arctic are estimated to host around 1500 Pg C, about 40% of total terrestrial soil carbon [53]. Carbon stocks are particularly concentrated in the 1.2 million km^2 of deep soils of the Yedoma regions of Siberia and Alaska (210-460 Pg C), and in Arctic river deltas (91±39 Pg C), with the remaining stocks (1035±150 Pg C) being spread across the broad surface permafrost pool (0-3 m, **Fig. 1**). There are likely to be additional poorly described deep carbon stocks (~400 Pg C). In summary, the total known pool of terrestrial permafrost carbon in the northern permafrost zone is 1330-1580 Pg C [53]. These stocks are similar in magnitude to the total soil carbon stocks in all other (excluding Arctic and boreal zones) biomes (2050 Pg C), and greater that the total estimated carbon stock in live vegetation (~1000 Pg C).

Incubation experiments and associated modelling efforts [53] suggest that 5-15% of permafrost carbon reserves would be emitted over the 21st century under a Representative Concentration Pathway (RCP) 8.5 scenario [the pathway that best captures "business-as-usual" greenhouse emissions pathways; [54]]. Assuming 10% loss and a permafrost carbon stock of 1450 Pg C, this is equivalent to 145 Pg C, or an annual rate of 1.45 Pg C yr^{-1} if spread evenly over the 21st century. Local emission rates vary depending on many factors, including *in situ* carbon stocks, local warming and thawing rates, degree of waterlogging (which influences the relative importance of faster aerobic *vs.* slower anaerobic processes), and soil carbon-nitrogen ratios. Averaged over the permafrost zone (excluding Antarctica, about 13-16 million km^2, we take 14.5 million km^2), and assumed a constant rate of release over the century, annual emission rates would be 100 gC m^{-2} yr^{-1}. In high carbon stock zones such as the Yedoma region, these rates may be substantially higher. These rates are based on gradual warming and decomposition scenarios –there is increasing awareness and concern that non-linear abrupt thaw events may approximately double the rate of release of CO_2 to approximately 200 g C m^{-2} yr^{-1}[50]. Indeed, abrupt permafrost thaw in ice-rich cold permafrost regions has already been observed [55]. Moreover, it is estimated that associated emissions of CH_4 will add an additional 25% (in mineral soil) to 45% (in organic soil) of radiative forcing effect over the next century [53]. On the other hand, increased woody vegetation growth in warming Arctic zones may act as a carbon sink, but also as an agent of radiative warming because of reduced surface albedo [56]. A number of studies suggest the net effect of increased woody vegetation in arctic and boreal latitudes is one of warming [57]. Estimating the opposing effects carbon and radiative forcing effects of woody vegetation increase is beyond the goals of this initial scoping, and for the present purpose we neglect the effects of woody vegetation, while noting that the net effect of preventing woody vegetation spread (e.g. through megafauna) is likely to be one of cooling [57] (see **Supplementary Material**).

Allowing for scaling factors for abrupt thaw events and the CO_2 equivalent effects of CH_4 (taken to be uniform across all zones), we estimate total annual permafrost carbon emissions of 300 g C m^{-2} yr^{-1}, or 4.35 Pg C yr^{-1} over the permafrost zone over the 21st century, increasing to 600 g C yr^{-1} over the Yedoma zones. While these calculations are crude and hence represent an initial approximation, they do suggest that the potential emissions from permafrost warming are larger than annual emissions estimated from current or projected land use change (~ 1-2 Pg C yr^{-1}), but smaller than those from fossil fuel emissions (currently

9-10 Pg C yr^{-1}) [58]. These numbers suggest that Arctic carbon emissions and associated land use options to deal with them warrant at least as much attention as land use considerations in other biomes that currently receive much greater attention. Moreover, the Arctic is warming very rapidly, and Arctic ecosystems are already changing at a fast pace in response. A "do nothing" or "leave as is" approach to managing these ecosystems does not imply that they would remain unchanged in their previous late Holocene state.

4. Arctic Megafaunal Ecological Engineering as a Nature Climate Solution

4.1. The mammoth steppe and climate change

The Pleistocene mammoth steppe interacted with the Earth System differently to the current wet tundra/forest tundra. Key differences relevant to the thermal regime and carbon budget, and hence climate change mitigation, are:

1) Grassland-dominated ecosystems have more reflective surfaces than shrub-dominated tundra and forest-tundra, both because of vegetation type and exposed snow cover, and thus enhanced albedo [26];

2) Snow trampling in winter by large herbivores as they move and forage for food implies a more compact snow layer and reduced surface insulation from very low winter air temperatures, enabling colder and deeper winter soil freezing [26];

3) *(2)* is enhanced by the lack of snow-trapping by shrubs and trees [59, 60];

4) Increased evapotranspiration of graminoids promotes lower soil moisture and decreases waterlogging [23, 26];

5) Large herbivore densities increase nutrient cycling and productivity by orders of magnitude, as the death-and-slow-composition nutrient pathway is overwhelmed by the herbivory-and-egestion pathway [23];

6) The root structure of grasses and forbs –they both have deep, diffused roots, contrary to the shallow root systems of tundra shrubs and larch– increase soil carbon storage in the first 1m [21].

Together, these mechanisms imply that mammoth steppe systems resulted in ***i)*** colder annual soil temperature driven by enhanced winter freezing, ***ii)*** enhanced albedo, ***iii)*** enhanced carbon capture and storage given increased productivity and deeper roots, and ***iv)*** reduced waterlogging. This implies an enhanced protection of the carbon-rich permafrost, with consequently reduced carbon emissions from permafrost thaw, increased carbon capture, and an overall negative feedback to global warming. Indeed, modelling studies suggest that the

LP/EH transition to tundra and forest-tundra altered albedo and may have contributed to regional and global warming at that time [15]. Considering that the shift from grasslands to moss-tundra was likely a consequence of reduced herbivore densities (see *Section 2*) that can be reversed [21, 61], restoring a proxy of the mammoth steppe ecosystems could stabilise –or at least delay– Arctic permafrost carbon release [27]. Thus, an ecosystem-based solution based on the introduction of megafaunal herbivores as ecosystem engineers is worthy of evaluation.

4.2. The Megafaunal Engineering Guild (MEG)

In order to consider the feasibility of enabling a phase shift from wet/moist tundra to a mammoth steppe-like ecosystem through enhanced herbivory, it is necessary to estimate a density and diversity of large herbivores able to enact and maintain it. In the following quantitative thought exercise, we will assume that a target state for each km^2 of converted/reverted Arctic mammoth steppe is comparable to the population density inferred from Pleistocene Arctic sites: we term this a *Megafaunal Engineering Guild* (MEG).

Target MEG density. Assuming that animal density in the mammoth steppe can be estimated from the number of bones found in the permafrost, an estimated average of 1 mammoth, 5 bison, 7.5 horses, 15 reindeer, 0.25 cave lions, and 1 wolf per 1km^2 roamed the area surrounding the site of Duvanniy Yar, an eroding bank on the lower reaches of the Kolyma river in north-eastern Siberia that has been exhaustively studied (**Fig. 2a**). These estimates are based on length of the soil exposure, thickness of Yedoma, rate of erosion of the soil exposure, density of bones per m^3 of soil column, the time period over which the soil was accumulated (42,000ka to 13,000ka in Duvanniy Yar), and the average age of the animals at the time of death. If we account for the average weight of adults for each species, the system sustained ~10.5 Mg of herbivores/km^2 [26]. We can expect heterogeneity in the above density values across the vast expanses of the Pleistocene mammoth steppe. However, commercial tusk collection data from Yedoma in different regions suggest similar numbers for mammoth [26], and multi-taxon herbivory values in Mamontovy Khayata –another intensively exposure east of the Lena River Delta, as well as in the New Siberian Islands are roughly similar to those in Duvanniy Yar [62]. In fact, data from multiple sources suggest herbivore biomass values ranging between 8.8 and 10.5 Mg of herbivores/km^2, with even greater values in Great Britain in last interglacial [30], suggesting that herbivore density values might have been even higher in past interglacials, since improved climatic conditions would translate in higher productivity. These values are within the range of present-day African savanna game reserves, 0.9-19.1 Mg of herbivore / km^2 [30].

MEG composition. Since mammoths and cave lions are not available in the near future, and reindeer and wolf are currently present in the Arctic, we focus our thought experiment on the potential introduction of bison and horses as the likely essential megafaunal engineers: bison to open up woody vegetation and horses to maintain grasslands (**Fig. 2c,d**). Apart from being present in the tundra already, reindeer/caribou are known to favour land cover transitions to grasslands [21]; however these shifts occur only at very high densities where these animals have been managed with fences in small areas (e.g. in reindeer pens) or across migration routes along linear features in the landscape [63]. In this respect, they are not considered an ecosystem engineer of the same calibre as bison or horse. Both horse and bison were abundant in the high latitudes during the Pleistocene and currently exist at high latitudes (e.g. bison in Alaska, horse in Yakutia and Alaska). American bison diet consists mostly of sedges and grasses, with a seasonal contribution of woody plants – mainly deciduous shrubs such as willow in summer [64]. This alone would favour the conversion to a savanna-type system of many deciduous-shrub dominated tundra regions. The closely related European bison is known to strip bark and open up closed forest [3, 30], showing equal preference for oak (deciduous broadleaf) and spruce (conifer) [65, 66]. Metabarcoding studies highlight the varied nature of the bison diet, highly rich in woody species [in some cases 48.6 to 51.9 % of their summer diet are trees and shrubs; 67], suggesting that the traditional understanding of bison diet might be limited by the current limited distribution of habitats it currently inhabits. This is in agreement with palaeo-ecological evidence, which gives an important role to bison (both American and Eurasian) as a first-order ecological engineer opening the landscape through its effects on woody vegetation [30]. Indeed, an examination of American bison palaeo-diets across its former continental-wide distribution through dental wear patterns showed a much wider dietary range and evidence of more activity on woody material than at present [68]. Horses are known to be strict grazers able to maintain grazing lawns but requiring other guilds to convert a woody landcover into a grass-dominated one [e.g. 69]. We did not include musk oxen in the MEG scoping experiment because –although they are known to be important extant megafaunal ecosystem engineers– they were not found to be abundant across the Yedoma region during the late Pleistocene [26], and they exist in low numbers at present and thus are not readily available for an Arctic *MEE* initiative.

It is important to consider whether mammoths are necessary for creating and maintaining the mammoth steppe. Mammoth has been estimated to directly consume a minor portion of the grassland productivity [<20% in Duvanniy Yar and Wrangel Island; [26]]. Due to this, it is hypothesised that although it most likely acted as a keystone species limiting the expansion of trees, this function was most important in the southern parts of the mammoth steppe, whereas in Arctic regions ungulates were probably able to maintain the "mammoth" steppe even in the absence of mammoths [26].

MEG growth rate. Little information is available on growth rates of translocated herbivores. The European Wildlife Bank (https://rewildingeurope.com/european-wildlife-bank/) uses a general growth rate for all large herbivores (irrespective of type) of 25% a year. However, this figure is an upper estimate based on ideal release conditions. Following discussions with Rewilding Europe experts and review of efforts to re-establish bison in Romania, an annual growth rate 10% per year is probably more realistic. This 'first estimate' growth rate could be refined in a hypothetical experimental phase, and finessed to account for effects of acclimatisation and herd size.

MEG growth model. We next estimate the potential dynamics of rate of megafaunal introduction and expansion, with the aim of evaluating how feasible it is to generate an ecosystem shift that is *i)* potentially economically viable in terms of carbon benefits, and *ii)* of sufficient scale to play a significant role in climate change mitigation.

First, we assume that the required animal density to engender and maintain Arctic grassland is 1 MEG/km^2 (i.e. estimated late Pleistocene animal densities: 5 bison and 7.5 horses km^{-2}). For the purposes of the model exercise, we assume that the herds are in place and the transition has occurred at $t = 0$, or occurs fast, and hence the effect on permafrost starts immediately (see *Section 4.5* and **Supplementary Material** for more on this assumption).

$\frac{dN}{dt} = I(t) + bN(t)$, where N is the number of MEG units at time t, $I(t)$ is the annual rate of new animal introduction (in MEG units), and b is the annual intrinsic population growth rate (10% yr^{-1}; see above).

If new mammoth steppe successfully prevents warming-related carbon loss from tundra, it generates an annual carbon benefit of c Mg C km^{-2} yr^{-1}. Converted mammoth steppe keeps yielding carbon benefits (avoided annual C emissions) every year after conversion, so the carbon benefit needs to be integrated over time. Hence, the carbon benefit of megafaunal introduction is C. Assuming the carbon benefit $c = 300$ Mg km^{-2} yr^{-1}(see *Section 3*), the net carbon benefit is therefore

$$C = \int_{o}^{t} c\,(I(t) + gN(t))dt$$

We explore numerical solutions of this equation for two scenarios: *i)* a constant animal introduction rate of 10 MEG yr^{-1}; *ii)* a ramping up introduction rate starting at 5 MEG yr^{-1} in the first year and increasing by 5 MEG yr^{-1} each subsequent year. Under the first scenario, after 30 years, an area of 3100 km^{2} would be converted to grassland, resulting in 1.8 Mt of avoided carbon emissions from avoided/delayed thawing permafrost. Assuming a carbon price of \$5 MgC^{-1} (see *Section 4.5* for details on the carbon price estimate), this results in US\$9 million of carbon income. Under the second scenario, the area converted to grassland after 30 years would be 8300 km^{2}, resulting in 4.7 Mt of avoided carbon emissions, and US\$23.5 million in carbon income. Hence, it is apparent that megafauna-based conversion to mammoth steppe may yield substantial income in a carbon market. However, implementing such projects to a scale that is significant for global climate would be a challenge. Conversion of 1.5 million km^{2} of Arctic tundra (10% of the Arctic permafrost zone) in 30 years would result in 850 Mt C of avoided carbon emissions, which would be significant in terms of global climate, but would require an introduction rate of 10,000 MEGs yr^{-1}, which is unrealistic. Hence the challenge of scalability is a major one.

4.3. The Pleistocene Park Experiment

The Pleistocene Park experiment in northeast Siberia (**Fig. 2b**) offers information on the practical feasibility of large-scale *MEE* in the Arctic. Sergey Zimov [14] first proposed the idea that reconstructed grassland ecosystems could prevent permafrost from thawing and thereby mitigate climate warming. Pleistocene Park (68°30′48″N 161°31′32″E) was first established in 1996 with an initial 40 ha fenced area, now nested within a new 100 ha fenced area established in 2018, and surrounded by a still larger 20 km^{2} fenced area established in 2005/6 –the total area owned being 160 km^{2}. The park offers a model to design experiments to test hypotheses along with practical information that can be used to outline the costs and logistics of large-scale arctic *MEE*.

The mammoth steppe biome was the product of interactions between vegetation and an assembly of large-bodied herbivores. The broad-range of body sizes and diet preferences had a strong effect on woody and other vegetation [30]. Different large herbivore species have different feeding strategies that generate inter-specific benefits through differential impacts on vegetation. Some permafrost dynamics are seen as a temporary practical advantage for the intended ecosystem phase shift: ice wedge degradation leads to surface subsidence, disturbing extant ecosystems and exposing bare soils that are rapidly colonised by grasses. This already ongoing process emits large quantities of carbon, but facilitates the introduction a guild of large herbivores which may maintain the new open landscape, prevent the regrowth of woody vegetation, and stabilise permafrost, hence delaying or stopping further emissions. Likewise, drainage of standing water bodies due to permafrost degradation [70] allows for new sites where grass initially grows and hence where large herbivores can be easily introduced. Indeed, a lake was artificially drained in Pleistocene Park to this effect (**Fig. 2e**). Mammoths apart, the complementary interaction between equids and bovids is considered a key driver of shifts to more open grassland landscapes. The ability bovids (ruminants) to digest cellulose present in leaves, bark and fibrous grasses opens and suppresses woody vegetation, whereas equids (non-ruminants) nibble less fibrous vegetation and promote short grass growth. Together, bovids and equids create and maintain ‘grazing lawns’ that are expected to maximise the albedo effect (see *Section 4.2*). Experience in the Pleistocene Park also suggests that horses are better able than bovids to plough and trample through snow to expose winter forage.

The primary focus of Pleistocene Park is to establish an ecosystem where a variety of herbivore species (including the horse-bison grazing interaction in association with feeding strategies of extant reindeer and elk) drive vegetation dynamics and foster a diverse and productive grassland system, with the eventual incorporation of predators and the generation of heterogeneity through landscapes of fear. Bison are preferred over cold-adapted cattle (e.g. Kalmyk cattle) because, as intermediate grazers [71] they switch between a woody plant and fibrous grass diet and have the build, power and behavioural traits to create clearings. Horse and bison populations disappeared from northern Siberia during the mid-Holocene. However, between the 13th & 17th centuries, horse-riding Yakut people moved into the region and their horse rapidly evolved anatomical, morphological and physical adaptations to thrive in the open year-round and grazing on vegetation below deep snow for 7- 8 months [72].

The park has struggled to establish significant numbers of animals due to the cost and logistical challenges associated with sourcing and translocation, and with keeping newly arrived animals alive over winter as a sufficiently productive grassland ecosystem has taken time to generate. As of October 2018, Pleistocene Park had 27 Yakutian horses, 1 bison, 4 musk ox (all male), 10 elk, 25 reindeer, 20 sheep, 9 yak, and 20 Kalmyk cattle. A further 12 American bison were translocated from Denmark in June 2019 at a cost of $110,000. The difficulty and cost of sourcing bison prompted the Park to experiment with cold-adapted domestic species from the Lake Baikal region (4,000 km to the southwest, **Fig. 3**), but initial trials have proved disappointing as the animals appear to avoid woody vegetation. To speed up the transition to grassland, serious consideration is being given to the option of seeding and fertilizing areas to create ‘founder grasslands’ that would act as ‘soft release’ areas for newly translocated animals. The grass seed pool is poor in present and undisturbed soils, where establishment may involve ‘pairing’ a MEG with a grasslands seed mix, which is important when considering expansion and scalability.

Due to its remoteness from large-herbivore populations, Pleistocene Park has yet to establish herds of sufficient density to rigorously test the megafaunal phase shift hypothesis. Nonetheless, progress to date has generated important knowledge, insight and evidence relevant to an assessment of the feasibility of establishing grasslands at scale. Initial monitoring data with belowground temperature sensors has shown a maximum difference of 14ºC in a heavily grazed fenced area *vs.* a control area (-24ºC *vs.* -10ºC at 25 cm, -20ºC *vs.* -9 ºC at 50cm, -16ºC *vs.* -8ºC at 90cm; March 2018), but more importantly, mean soil annual temperatures 2.2 ºC cooler in grazed areas, as well as increased carbon sequestration in the first 1m of soil in grazed areas [73]. Furthermore, Pleistocene Park has developed practical knowledge on the logistics of translocating animals, and generated creative and grounded insight on herbivore ecology and future strategies for scaling-up. Lastly, the fact that one family in a remote location has successfully overcome major translocation challenges with their own resources only suggests that an organised and properly financed effort could achieve major impact.

4.4. Strategy for creating a rolling frontier

Large-scale *MEE* would require an experimental, design and socialisation phase followed by an implementation phase. We envisage that the first phase would comprise three components that could be completed within 10 years: ***1)*** Establishment of a trans-Arctic network of experimental reserves. Based on Pleistocene Park experience, we estimate that rigorous hypothesis-testing would require enclosure experiments involving around 1000 bison and horses; ***2)*** Modelling and planning a 'rolling frontier' that integrates biophysical, ecological, cultural, administrative and logistical considerations in its design and generates authoritative carbon budget predictions; ***3)*** Policy and public dialogues to generate interest, acceptability, buy-in and the new policy mechanisms that an initiative of this scale and novelty would require (see *Section 4.6*).

The design of a rolling frontier could take inspiration from the migration and settlement strategy of the early Sakha Turkic people to northern Siberia since at least the last 500 years: they exploited the natural thermokarst dynamics, settling in thermokarst depressions or drained thaw lake basins –known as *alas*– often draining the lakes themselves, where their horses and cattle maintained grass growth to form pastures [74]. Ongoing permafrost thawing accelerates thermokarst processes: as mentioned before, disturbed soils due to ice wedge degradation and drained water bodies offer prime opportunity areas to target within this *MEE*, since they facilitate the rapid establishment and expansion of grasslands. Moreover, integrating the affordance of technology into the design could further accelerate the expansion of the megafauna frontier and also make it a more attractive investment. For instance, integrated information system (ISS) designs involving remote sensing, satellite tracking of animals, carbon flux sensor networks and climate modes could enable regional-scale environmental monitoring. In addition, ISS-generated change-of-state metrics could interface with blockchain platforms to generate verified carbon credits and/or action smart contracts for payments associated with poof of action/impact [75]. This would dramatically reduce operational transaction costs thereby increasing the prospect of investment returns: a bison blockchain pilot is already underway in Romania and planetary satellite analytics are undergoing a step-change in terms of resolution, power and cost (https://rewildingeurope.com/).

4.5. A first-cut business plan for Arctic *MEE*

We have calculated an approximate cost of the bison, horse and reindeer component of a MEG. We have included reindeer in this costing exercise because they are available for purchase, they have a distinct ecological niche and function, and their inclusion would increase the speed of the experimental and establishment phases, although since they are present in most Arctic lands, their introduction might not be required in some cases. We estimate an experimental 10-yr implementation cost of 1 MEG to be US$383,000. This figure includes costs on animal purchase (5 bison, 7.5 Yakutian horses, 15 reindeer), translocation (transport, permit fees, food), introduction (fencing and other infrastructure, winter fodder, husbandry for 10 years). The figure is derived from a combination of local price knowledge of horse and reindeer and experience of translocating large herbivores to the Pleistocene Park, 2018 US bison auction prices, and a rough quote for airfreight bison from Chicago to Magadan from a leading livestock transport firm. The cost assumes that bison will be sourced from North American ranches in shipments of 120 (= sole freight charter) which brings down costs, but would require minimum investments of 24 MEGs (i.e. US$9.2million). It does not take into account the likely increases in prices that a high demand for these animals might create. We assume that over time (10-25 years), and as herds build up, prices will drop and compensate for higher initial purchasing costs. This is a rough estimate figure with scope for refinement and financial modelling.

The cost of establishing an experimental Arctic *MEE* area (comprised of ~1,000 bison + horses, ~80 MEG – see *Section 4.4*) would be US$30.5million. Scientific infrastructure, research personnel, and area management would cost in the order US$0.75million per year, such that each 10-yr experimental area would cost US$38 million. An experimental *MEE* area would generate key empirical knowledge on the effects of *MEE* on the ecological and Earth system processes discussed above, but it would also be designed to produce practical knowledge on logistics, and on how to create an efficient rolling frontier strategy appealing to investors.

These areas might generate cost recovery in terms of carbon sequestration. In the following calculation an estimate of market price of US$5 MgC^{-1} is used. This figure is a compromise between the 2018 US$10 MgC^{-1} midpoint value of carbon pricing in compliance market (Word Bank 2019) and the 2017 average of US$3 MgC^{-1} in voluntary market initiatives [76]. Carbon prices are likely to rise in the near future as more countries, sub-national governments and corporations commit to ambitious net carbon emissions goals as part of their Paris climate goals, and *NCS* are incorporated within those targets. If an Arctic *MEE* was established in Russia, generated carbon credits would likely to be traded on the voluntary market because Russia lacks a carbon tax and hence a pricing mechanism. It is currently a buyers' market, where the value of credits depends on factors beyond carbon, such as country of origin and, importantly, the story of their generation. Using the estimated carbon benefit of 300 Mg C km^{-2} yr^{-1} MEG^{-1}, once an experimental area reaches full impact, it could generate up to 24,000 Mg C yr^{-1} and US$120,000 yr^{-1} in carbon revenues. This would represent a 0.32% (0.4% without research cost) annual return – i.e. financial benefits expressed as a proportion of the invested capital – on investment after 8-10 years (the implementation phase over which the herd would establish and change vegetation cover substantially to affect permafrost).

It is perhaps unfair to judge the appeal for investment of Pleistocene Arctic *MEE* in the light of the experimental phase annual returns. Once this phase is completed, and assuming that *i)* MEGs establish and maintain a phase shift to a grassland-herbivore system, *ii)* source herds develop, and *iii)* an efficient roll-out strategy is designed, a business case for Arctic *MEE* could look promising. Annual revenues for Arctic *MEE* initiatives post-experimental phase would increase in proportion to their cost efficiency in relation to the experimental *MEE* areas (i.e. 1/3 of the initial experimental cost would translate in revenues >1% yr^{-1} after 8-10 years). Returns could be significantly increased if/when Arctic countries introduce a carbon tax and pricing mechanism. Whilst we recognise that these figures are approximate and contain many assumptions (see **Supplementary Material** for further discussion on this), they do enable us to generate an order of magnitude figure for *MEE* in the Arctic under the framework of the global carbon budget. This is US$114million for feasibility testing if we consider 3 experimental Arctic *MEE* areas over a period of 10 years.

4.6. Institutional Friction

Even with available funds to test, design and develop Arctic *MEE*, there would still be significant institutional challenges to overcome. Institutions are assemblies of rules, norms, worldviews, discourses and practice structures that shape (constrain or enable) the possible in the social and political realm [77]. Institutions order society and are embedded in the political economy. This creates powerful forces to retain the status quo: deviance from the established way of doing things is often perceived as unsettling and undesirable by influential publics, both political and social. From an institutional perspective, the concept of large-scale megafaunal engineering outlined here is radical in almost every dimension. As a result, its development and implementation are likely to generate considerable institutional 'friction' at all levels. In the geo-political realm, Arctic regions such as Russia, Alaska and the Canadian Yukon would be providing a global public good (avoiding large carbon emissions), which would add a major new dimension to international relations. In the bureaucratic realm, the bison and horses would become a new category of wildlife that is neither fully domestic nor wild. Veterinary and livestock institutions generate significant power and rents from managing disease in domestic herds through animal movement controls. Negotiation of a transnational 'deal' with these institutions would be necessary to support movement of animals at the scale required. In the realm of intellectual and popular discourse, the idea of transforming large portions of the Arctic with livestock is likely to prompt comparisons with the Lysenkoism agriculture of Soviet era Stalinism that produced famines killing millions [78], and claims that it is a neo-colonial project that frames the Arctic as a free un-populated resource for others to appropriate. Nevertheless, we anticipate that societies at large will likely be more open to direct interventions in nature (e.g. geoengineering) in order to adapt to or mitigate climate change in the near future as climate change impacts increase.

5. Discussion & Conclusions

In this study, we explored if Pleistocene-inspired Arctic *MEE* is viable and could be scaled up to play a significant role in global climate change mitigation. Whereas we found it to be reasonably viable economically, our results suggest that ramping it up to a scale likely to be a significant contribution to global climate change mitigation on its own would be a challenge, since the numbers of large herbivores required for such an undertaking do not exist. Nevertheless, such initiatives might avoid high carbon emissions where and when implemented, especially over Yedoma permafrost soils.

Our quantitative scoping exercise aimed at providing for the first time a rough estimate of the feasibility of such an approach. It is based on a number of assumptions, which are discussed at length in **Supplementary Material**, and which comprise *1)* determining an effective megafaunal density and guild; *2)* the immediate effect of a MEG on the landscape; *3)* effectiveness of the mammoth steppe on thermal, nutrient, and carbon budget; *4)* the MEG growth rates; *5)* the size of the experimental units; *6)* the role of predators; and *7)* the price of carbon. Together, they make a compelling case for a systematic monitoring and the implementation of a plan as described in *Sections 4.4-4.6*. Our essential assumption is that Arctic *MEE* is effective to protect permafrost and delay its thaw. There is ample palaeo-ecological and empirical evidence to assume that the sequence of processes and the net effect of Arctic *MEE* discussed in this study are plausible, although we did not aim at testing them but at analysing the feasibility of such an action assuming that they work. All other assumptions follow from this and have been conservatively applied according to values obtained from the literature.

Ongoing climate change-caused rapid permafrost degradation is creating thermokarst lakes that enhance carbon emissions, but also enhancing the drainage of water bodies through catastrophic drainage [e.g. 70] and land subsidence that causes disturbance, exposing fertile soils and creating grazing landscapes over large areas that could be readily used in Pleistocene-inspired *MEE* actions taking past Sakha horse and cattle herders' land use techniques as an inspiration [74]. Our approach did not incorporate the increase in carbon capture and storage by the more productive, deeper-rooted grassland community [73] and thus underestimated the carbon balance by neglecting increased soil carbon capture.

Our first cut business case estimate assumed that governments and groups with title or claims over land would choose to sponsor such large-scale landscape changes (i.e. it did not cost land): many ongoing *MEE* initiatives work this way (https://rewildingeurope.com/). Since our economic feasibility plan only focused on the carbon market, it did not include other co-benefits that might arise such as employment, new tourism economies, carbon-negative wild meat, and other carbon-negative products. This could potentially enhance *substitution effects* – e.g. reduced demand for beef and thus reduced pressure on forested areas in tropical regions, although this later point would require a thorough consideration on the socio-economic consequences of geographically shifting economic activities. In any case, the finding that this initiative is viable offers an opportunity but also potential friction that might need being negotiated at the local scale.

Considering safeguards to avoid perverse outcomes for existing Arctic biodiversity is pertinent given the scale at which such initiative could take place. In this respect, ~42% of the pan-Arctic tundra region has been deemed susceptible to such changes [23], and a much smaller extent than this is estimated to be within reach of such ecological engineering within the next decades given scalability issues (this study). Even the regions where such transition would occur would be heterogenous, with a diversity of vegetation cover according to topography as it likely was in the Pleistocene [26]. Moreover, no arctic or alpine plant species with a fossil record has become extinct in the Quaternary [79], the only well-documented

Pleistocene extinctions in the Arctic being those of the megafauna. Hence, even though the shift would represent a large re-balance of species abundances regionally, there are no signs that it could carry over increased extinction risks for current Arctic biota.

In summary, our analysis suggests that land use change in the Arctic has similar or greater implications for climate change and the carbon cycle than other regions at lower latitudes where land use issues receive much more attention. Irrespective of what action we take, terrestrial systems in high latitudes will influence the character of global climate change and, given current rates of warming, will not remain unchanged under a 'do nothing' approach. Although there is debate on the role of human agency in *LP/EH* extinctions [e.g. 80], and thus in the consideration of current Arctic terrestrial systems as defaunated or trophically downgraded, the weight of evidence is in favour of a decisive role of human over-hunting in the demise of many megafaunal species. Regardless of the cause, there is ample evidence of the role of large herbivores on the region's ecological and biogeochemical processes. If this initiative is to work, a large experimental phase would need to be implemented for generation of empirical data, and logistics and practical knowledge. We invite expertise from all disciplines –e.g. livestock breeding, financial modelling, ecology, social sciences– to collaborate in determining the feasibility of such a mammoth task.

6. Figure Captions

Figure 1. (a) ***Shades of brown:*** estimated Soil Organic Carbon storage (kg C m^{-2}) in the 0–300 cm depth range of the northern circumpolar permafrost region. Data normalised for total polygon area (including non-soil areas) [81]; ***Pink regions***: areas of deep, organic-rich Yedoma deposits [47]; ***Green line***: tundra/boreal forest treeline [82]. **(b)** ***Dashed area***: areas of treeless Arctic tundra –any land north of the Arctic treeline [82]– and 'Oro-Arctic' areas [83]; ***Shades of green***: map of selected areas with defined tree canopy cover over the circumpolar taiga-tundra ecotone. Derived from the 500-meter MODIS Vegetation Continuous Fields (VCF) product as averaged over six years from 2000-2005 and processed as described in [84]. It depicts patches of low tree canopy cover indicative of the forest-tundra ecotone. Map covers 60°N-70°N (Eurasia) & 50°N-70°N (North America). Map projection: Azimuthal Equidistant, geodetic datum: WGS84.

Figure 2. **(a)** Ice-rich Yedoma permafrost exposure in Duvanniy Yar, an eroding bank on the lower reaches of the Kolyma river in north-eastern Siberia. Note the small Dahurian larch – *Larix gmelinii* (Ruprecht) Kuzeneva 1920– trees on the top of the ridge, heavily disturbed by permafrost dynamics, the rich syngenetic ice-wedges, and the lush grassy vegetation on top of nutrient-rich detached soil fragments; **(b)** aerial view of a section of Pleistocene Park. The thick black line marks the outer fence of the area; **(c)** Yakutian horses in Pleistocene Park; **(d)** European bison browsing on *Alnus viridis* (Chaix.) D.C. shrubs; **(e)** herd of yaks grazing on a drained lake in Pleistocene Park.

Figure 3. Location of Pleistocene Park (inset) and the routes for transporting large herbivores from potential sources areas. See text for details.

7. References

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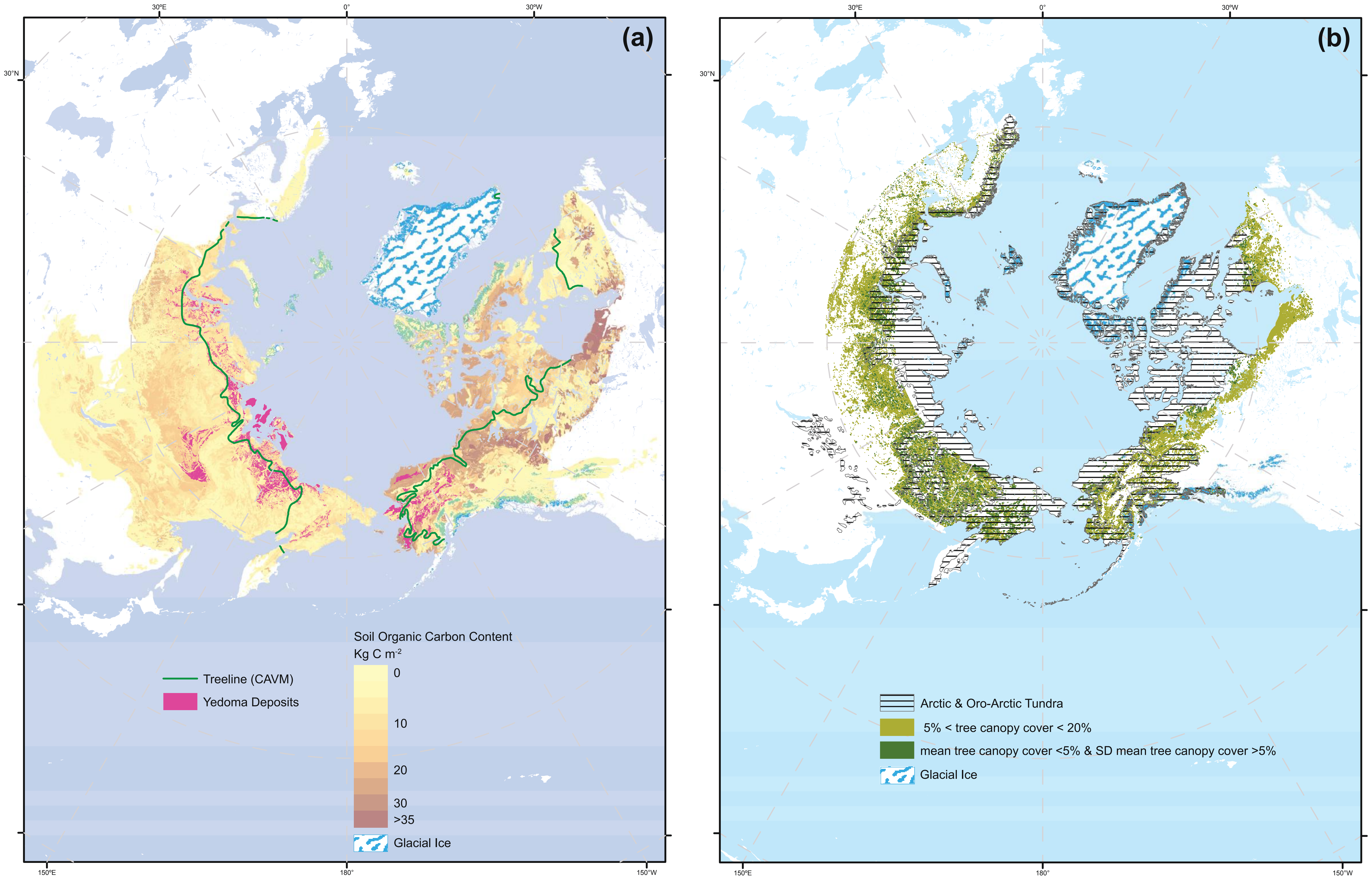

Figure 1. (a) ***Shades of brown***: estimated Soil Organic Carbon storage (kg C m−2) in the 0–300 cm depth range of the northern circumpolar permafrost region. Data normalised for total polygon area (including non-soil areas) [63]; ***Pink regions***: areas of deep, organic-rich Yedoma deposits [64]; ***Green line***: tundra/boreal forest treeline [65]. **(b)** ***Dashed area***: areas of treeless Arctic tundra –any land north of the Arctic treeline [65]– and 'Oro-Arctic' areas [66]; ***Shades of green***: map of selected areas with defined tree canopy cover over the circumpolar taiga-tundra ecotone. Derived from the 500-meter MODIS Vegetation Continuous Fields (VCF) product as averaged over six years from 2000-2005 and processed as described in [67]. It depicts patches of low tree canopy cover indicative of the forest-tundra ecotone. Map covers 60°N-70°N (Eurasia) & 50°N-70°N (North America). Map projection: Azimuthal Equidistant, geodetic datum: WGS84.

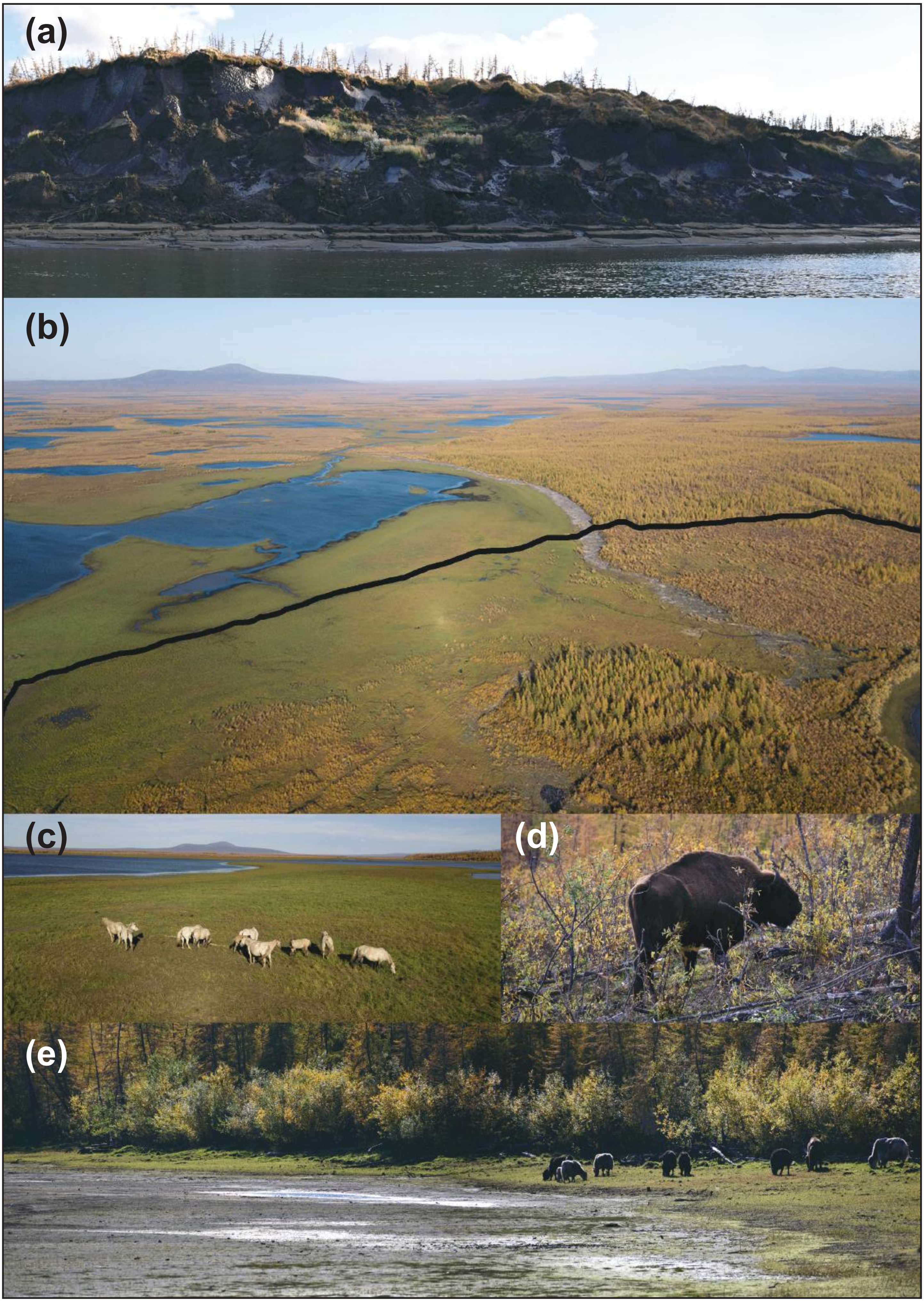

Figure 2. **(a)** Ice-rich Yedoma permafrost exposure in Duvanniy Yar, an eroding bank on the lower reaches of the Kolyma river in north-eastern Siberia. Note the small Dahurian larch –*Larix gmelinii* (Ruprecht) Kuzeneva 1920– trees on the top of the ridge, heavily disturbed by permafrost dynamics, the rich syngenetic ice-wedges, and the lush grassy vegetation on top of nutrient-rich detached soil fragments; **(b)** aerial view of a section of Pleistocene Park. The thick black line marks the outer fence of the area; **(c)** Yakutian horses in Pleistocene Park; **(d)** European bison browsing on *Alnus viridis* (Chaix.) D.C. shrubs; **(e)** herd of yaks grazing on a drained lake in Pleistocene Park.

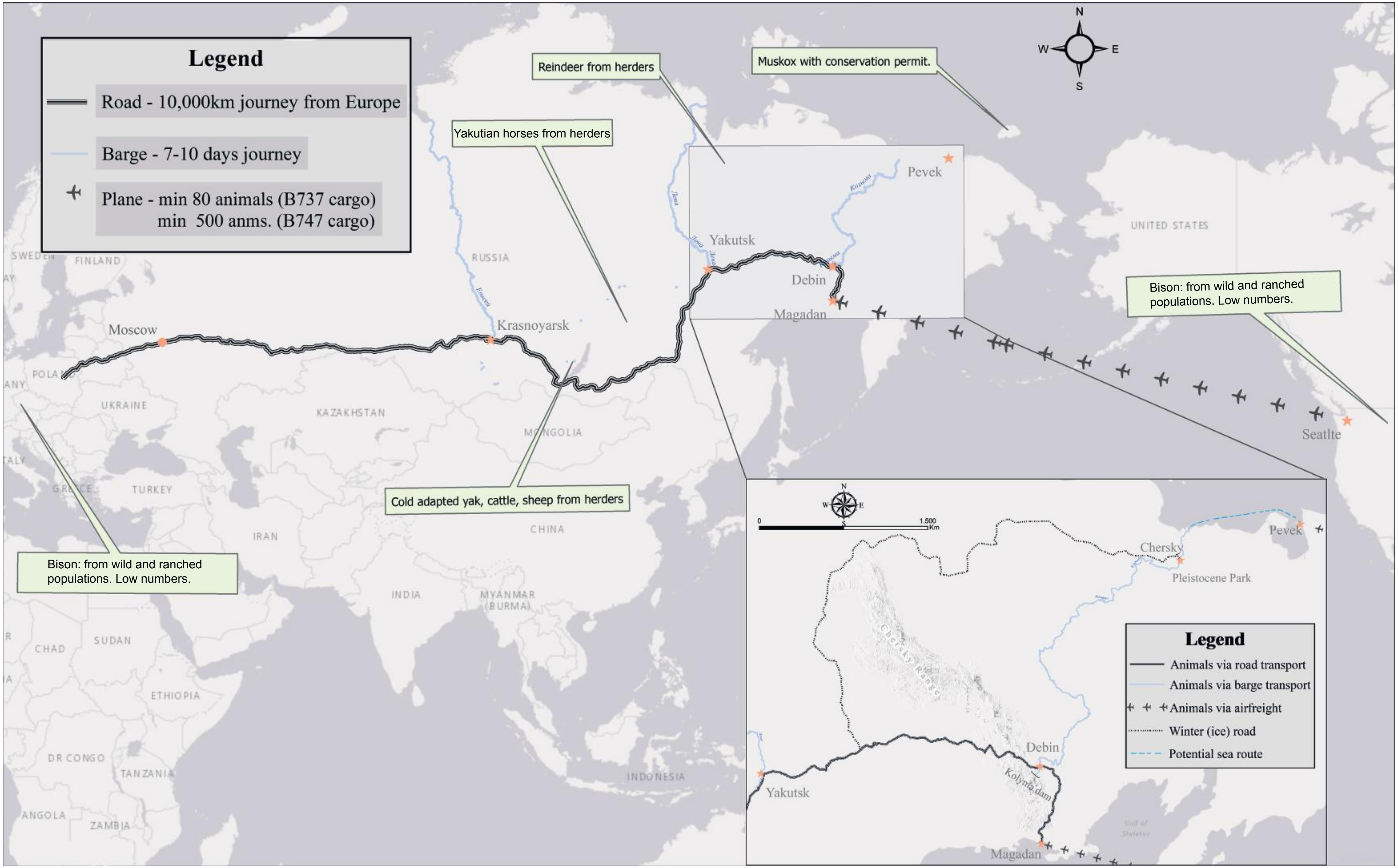

Figure 3. Location of Pleistocene Park (inset) and the routes for transporting large herbivores from potential sources areas. See text for details.

SUPPLEMETARY MATERIAL: PLEISTOCENE ARCTIC MEGAFAUNAL ECOLOGICAL ENGINEERING AS A NATURAL CLIMATE SOLUTION?

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The following section discusses the main assumptions/simplifications taken in this study and suggests future research to address the uncertainties stemming from them.

Assumption 1. *Reference Megafaunal Density*: the effective animal density is 1 MEG/km^2 (5 bison and 7.5 horse km^{-2}) and stems from estimated animal densities in Northern Russia in the late Pleistocene [1]. There is at present no experimental setup able to better constrain this number. Failing to achieve a density able to convert land would probably result in a net increase in greenhouse gas emissions.

Assumption 2. *Immediate conversion to grassland*: our quantitative exercise assumes immediate vegetation conversion and permafrost protection. As stated in *§4e*, in reality a period of time –estimated to be >8 years– will be required to achieve this state change. The animal density estimate of 1 MEG km^{-2} occurred in the late Pleistocene, in a region where large megafauna/soil/vegetation feedbacks had operated for millennia and thus with soils that were much richer in nutrients than those in current forest-tundra and tundra. Experience in Pleistocene Park suggests that nutrient limitation and seed availability are key in the early years of Pleistocene Arctic *MEE*. Without an initial management phase *–ranching kickstart phase–* which includes at least allochthonous winter fodder while the local feedbacks start enriching soils, high herbivore densities might not be self-maintained in the early years. After such phase, self-sustainable herds are anticipated.

Assumption 3. *Effectiveness of mammoth steppe on thermal, nutrient, and carbon budgets*: our MEG growth model assumes that in the short term grassland systems will effectively delay permafrost thaw. However, in the coming decades the efficiency of this cooling effect (measured as ~2ºC in annual average temperature) will eventually depend on climate warming. Ultimately, this *NCS* can delay permafrost thaw, but needs being implemented in conjunction with many other actions, most importantly reduction of greenhouse gas emissions. The net effect of Arctic *MEE* will also be determined by the following:

3.1 Initial greenhouse gas emissions from land vegetation removal: transitioning from wet moss/shrubby tundra and forest tundra to grasslands implies an initial loss of plant biomass. Epstein *et al.* [2] estimated a recent gain of aboveground biomass of 0.4Pg C in 3 decades due to tundra greening across the whole biome. Even if we account for twice this value by adding belowground biomass [3], the amount of carbon gained by increased shrub biomass is small at a global scale –see *§3*. Further, we need to take into account the fact that forbs' and grasses' aboveground/belowground ratio is smaller and their productivity higher. Berner *et al.* [4] estimated the overall aboveground standing biomass in the North Slope of Alaska to be 700 gm^{-2}, with 43% of such biomass attributed to tall shrubs (i.e. 300 gm^{-2}): compared with average 21st century emissions from permafrost ranging between 100 and 300 $gm^{-2}yr^{-1}$, this number could be offset in a short period with effective *MEE*, especially in Yedoma soils and if avoiding abrupt permafrost collapse. Initial emissions due to transport of animals and additional forage in the *ranching kickstart phase* should also be accounted for: these can be large, especially if animals need being air-freighted from other continents, although they are a one-off and should be rapidly recovered by an effective *MEE*. Quantifying these effects in detail requires considering the most carbon-efficient way to move the animals, as well as the overall carbon contained by the increasing biomass in the megafauna itself.

3.2 Methane emissions as a by-product of enteric fermentation by herbivores: methane emissions from megaherbivores are known to be large and are suggested to play (and to have played) a significant role in the overall CH_4 atmospheric concentration [5]. Given the very large efficiency of methane as a greenhouse gas, CH_4 emissions from increased populations of megafauna may contribute to enhanced warming. CH_4 production is estimated at 100 kg yr^{-1} Mg^{-1} of animal weight for wild ruminants –4.5 times smaller for non-ruminants [6]. Using the average mass of an adult bison (600kg) and that of an adult horse (400kg) [1], CH_4 emissions due to enteric fermentation by herbivores of 1 MEG (composed of 7.5 horses and 5 bison km^{-2}) would be 0.37 Mg CH_4 yr^{-1} km^{-2}, a value 4 orders of magnitude smaller than the overall carbon benefit estimated by the *MEE* (see *§3* and *§4b*).

3.3 The role of hydrology in greenhouse gas emissions: a central point in permafrost carbon emissions is the balance between emitted CH_4 and CO_2, in which hydrology plays a critical role. Thermokarst lakes and water-saturated areas with anoxic conditions are the main sources of CH_4 [7, 8]. Establishment of drainage networks decreases lake and standing water and leads many lakes to eventually drain, exposing unfrozen ground – *talik*, which may refreeze again if mean annual temperatures are <0ºC, but after having lost much carbon [7]. Thus, drier soils on permafrost have lower global warming potential than wet ones due to lower CH_4/CO_2 emission ratios [8]. Whether permafrost regions become wetter or drier in a warmer Earth was not yet been determined and constitutes a major research question [9], although we know that thermokarst lake formation was a large CH_4 source in the *LP/EH* and is likely to occur in a warmer planet in the ice-rich Yedoma regions [7]. Conversion to grassland through effective Arctic *MEE* would increase transpiration and contribute to drier land, thus reducing greenhouse warming potential. Moreover, it could also favour permafrost aggradation in drained lakes in areas within continuous permafrost [10]. The net effect of such action will depend on the difference between the effect of *MEE* on permafrost hydrology and the trajectory of these landscapes in the absence of any action.

3.4 Albedo effect: we did not account for the effects of albedo modification in the quantitative thought process presented in this study, however existing literature points to a significant reinforcement of the cooling effects of landcover change from wet moss/shrubby tundra to grass-dominated ecosystem when accounting for albedo [see §3; 11, 12]. A comprehensive energy budget on the net effects of Arctic *MEE* requires measurement of changes in radiative forcing (Wm^{-2}) due to albedo.

Assumption 4. *Herbivore growth model:* a 10% $year^{-1}$ growth was used from experience on re-establishing bison in Romania, and a lack of literature on growth rates of translocated herbivores was noted. Such estimates can be refined in the experimental phase defined in *§4d*.

Assumption 5. *Herbivore size of a MEE experimental unit*: 1,000 animals are considered sufficient for an experimental *MEE* area according to the experience of running Pleistocene Park. This number could be refined by modelling exercises as well as literature search on herd sizes able to enact ecosystem phase transitions.

Assumption 6. *The role of predators*: Pleistocene Park has excluded predators in an attempt to boost current herbivore numbers. Predators (wolf, possibly tiger) are expected to increase landscape heterogeneity by modifying herbivore behaviour and herd movement [13] –see *§2*. Inclusion of predators in experimental phases starting with ≥~1,000 large herbivores would be achieved early, as it is deemed crucial to avoid pockets of overgrazed terrain.

Assumption 7. *Price of carbon* (discussed in *§4e*). Given the wide range of values for carbon depending on whether these are obtained in compliance or voluntary market initiatives, we conservatively used carbon price estimates on the lower range of possible values.

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