Chapter 10
The Past and Future of the Mammoth Steppe Ecosystem

Sergey A. Zimov, N.S. Zimov, and F.S. Chapin III

Abstract During the Last Glacial Maximum (LGM) the mammoth steppe was the planet's biggest biome. Ice rich loess-like soils of this biome covered vast northern territories. These soils are currently one of the biggest carbon reservoirs. It is likely that in this century the bigger part of these soils will thaw. This would lead to massive erosion, destruction of modern ecosystems and a large emission of carbon dioxide and methane into the atmosphere, which are produced from the decomposition of Pleistocene organics. Minimizing these effects is possible only through the restoration of ecosystems similar to the Pleistocene mammoth steppe. Skeleton densities in the permafrost show that the mammoth steppe was a highly productive ecosystem similar to African savannas. Biomass of animals in the north of Siberia was ~10 t/km^2. Herbivores enhanced biocyclicity, trampled moss and shrubs and maintained pastures. Therefore this ecosystem was only partially dependent on climate. Analyses of climate dynamics, vegetation and animals shows that today the climate in the north of Siberia, Alaska and Yukon are close to the optimum of the mammoth steppe, and that climate warming did not destroy this ecosystem. Rather, humans are the more likely cause. After the LGM, climate warming allowed humans to penetrate the north, where they decreased animal densities to the point where they became insufficient to maintain pastures. In this chapter we discuss questions of preservation of bones and artifacts in the permafrost, physiology and evolution of pasture ecosystems and the role of humans in this ecosystem.

Keywords Extinction • Global warming • Humans • Mammoth steppe • Permafrost

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> *'If one had not seen this with one's own eyes, it would be impossible to believe that in these desolate areas there could exist such a large number of animals, congregating sometimes in herds of thousands. Only by wandering from one place to another could these large groups find enough feed on the meager grasslands of the wastelands. But the animals do not know their major enemy – humans, and the animals live wild and free, far away from bloodthirsty pursuit.'*
>
> N.M. Prjevalskii
> Mongolia and Tangut country (1873)

10.1 Introduction

According to IPCC reports, in this century alone the climate on the planet will become warmer by 2–7.5°C (Solomon et al. 2007). In the Arctic this change in temperature will be even greater, which will have a massive impact on northern ecosystems. Specifically, tundra ecosystems will give way to forests and polar deserts will in turn give way to tundra. But this will not be the only outcome. In the northern parts of Siberia, Alaska, and the Yukon, glaciers are few. In these areas vast plains, river valleys and mountain slopes have accumulated massive strata of loess or loamy soils. Sedimentation is slow – usually less than millimeters per year, but over the course of tens of thousands of years this has resulted in an accumulation of several tens of meters of loess (Schirrmeister et al. 2002; Sher et al. 2005; Zimov et al. 2006a). These layers are frozen and on average contain 50% ice, although in the far north of Siberia ice content can reach 90%. The biggest part of this ice is a polygonal network of ice wedges, which form as a result of frost cracking of sediments (Yershov 1998). The local name of such massive Pleistocene loess with ice wedges is *yedoma* (Fig. 10.1).

During interglacial periods the depth of the summer thaw increased and these ice wedges began to thaw. Depressions appeared, water filled these depressions, ponds appeared, which interflowed and migrating lakes (thermokarst lakes) were formed (Zimov et al. 1997; Walter et al. 2006). During the course of the Pleistocene-Holocene transition (PHT) this process eroded half of the yedoma (Walter et al. 2007). During the migration of thermokarst lakes creeks, ravines and rivers were encountered. When this happened, water escaped from the lakes, creating canyons. The lakes dried out and refroze, and new nets of polygonal ice wedges began to form.

With increased global warming the permafrost layer will again begin to thaw. It could be assumed that this will first occur next to southern permafrost boundary, where the temperature of permafrost is close to 0°C, rather than in northern Siberia, where permafrost temperatures are as low as −5°C to −10°C, such that global warming is not a thread to northern Siberian ecosystems. But that is not so. The top of the ice wedges in the north usually lay at a depth of only 0.5–1.8 m, with the depth of summer thaw (active layer) being 0.2–1.6 m (pers. obs.). Therefore in

Fig. 10.1 Part of Duvanii Yar, where the ice-wedge thaw is active. In June the river water level is high and the beach absent

some cases if the depths of the summer thaw increases by only 0.1–0.2 m, ice wedges will begin to melt, and the permafrost layers will begin to erode.

It can be imagined that the soils of northern Siberia are a subsurface "glacier" 10–50 m thick, which is protected from the summer sun with a thin soil layer. As one moves north the permafrost gets colder, but simultaneously the ice content increases and the thickness of heat-insulating soil cover decreases. For this region, it makes no sense to discuss the vegetation response to climate change – all vegetation would be destroyed. Modern soils would be mixed with yedoma soils; some would slide down to thermokarst lakes, some to creeks or rivers; this would increase their turbidity, and river and estuary ecosystems would be destroyed. Substantial portions of organics and mineral soils would be transported to the ocean, which would in turn accelerate sea ice thawing.

Besides regional effects, permafrost degradation will also affect global climate. Carbon storage in the top layer of permafrost is estimated to be $1{,}672 \times 10^{15}$ g (1,672 Pg) of carbon (Tarnocai et al. 2009). This is more than the amount stored in the terrestrial biomass and atmosphere combined. Permafrost is the biggest organic carbon reservoir. And the yedoma is especially carbon rich, with hundreds of kilograms C per m^2 (Schirrmeister et al. 2002; Zimov et al. 2006a). When the yedoma thaws microbes quickly transform this carbon into greenhouse gases. In aerobic conditions CO_2 is produced (Zimov et al. 2006b) and in anaerobic conditions (e.g. in the bottoms of thermokarst lakes, ponds and rivers) CH_4 is produced (Zimov et al. 1997; Walter et al. 2006). Microbial oxidation of carbon is accompanied by heat production, therefore when the organic rich systerm starts to thaw, the process becomes hard to stop (Chuprynin et al. 2001; Khvorostyanov et al. 2008), and the heat produced by microbes is enough to thaw the entire system. Greenhouse gas emissions from thawing permafrost would strengthen global warming which would in turn increase permafrost thawing; and the probability that bigger portions of the yedoma will thaw in this century is already high. Is there is a way to slow down permafrost thawing? Theoretically it is possible, but there are few options. In this chapter we discuss the reasons why one such option, namely the rewilding of extensive areas in northern Siberia, may hold the answer to the loss of this unique ecosystem.

10.2 Observations and Experimentations on Permafrost Thaw

Figure 10.2 shows our experimental permafrost thaw site. Initially a mossy forest was situated on this inclined slope, 8 km to the southeast from our station (Fig. 10.3). The depth of the summer thaw varies from 0.3 to 0.8 m. The tops of ice wedges are situated as deep as 1.6–1.8 m beneath the surface. In the beginning of the experiment the temperature of permafrost was −6°C to −7°C. In 2001, in an area covering 3 ha, the top organic layer of soil with a thickness of 0.2–0.3 m was removed with the help of bulldozer. The next year an additional 0.3–0.4 m of soil was removed over 1 ha. The removed soil acted as a heat insulating "coat" for the permafrost underneath, and the removal of this coat caused permafrost degradation. On the territory where only the top layer was removed 1.5–2 m of permafrost thawed over 10 years, however where there was additional removal, the permafrost thawed by 4–4.5 m.

Mechanical treatment in our experimental site is equivalent to 2–3°C of warming. This would not be enough for all the permafrost to thaw; however a substantial portion would. If the climate stays stable then the permafrost thawing in our experiment would slow down with time, as the ground slough would create an insulating cover for ice wedges over time. But summer temperature increases over the last years (more than 2°C for 20 years) accelerated the thawing of permafrost on our site.

If we were to repeat our experiment on a flat surface, then the permafrost would equally degrade; however there would be no drainage and the area would be covered with water – i.e., a thermokarst lake would appear. And if the slope were steeper then the thawing soil would flow down, sliding on slippery ice wedges. Frozen soil and ice would appear on the surface, which might accelerate thawing by up to 0.1–0.2 m per day. The zone of erosion would quickly occupy the entire slope. Down the slope a ravine would appear while up the slope a vertical, rapidly retreating cliff would appear. Active erosion would stop only when inclination of entire slope declined or when all ice wedges thawed.

The loamy soils and loess found in the north are very texotropic – the wet mineral soil can look solid, but subject to disturbance it quickly turns into a liquid mud. Figure 10.4 shows images of the inclined slope of the Filipovka River basin, 50 km to the northeast from our station. In 2002 there was natural fire, which increased the depth of the summer thaw. The top horizons of the ice-rich permafrost thawed, started moving and turned into a torrent. As a result all the thawed soil from

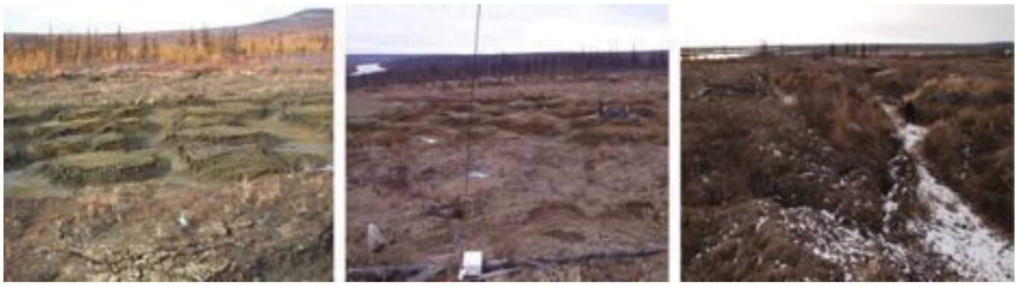

Fig. 10.2 On this gentle slope the organic layer of soil was removed with the help of a bulldozer. This has provoked degradation of permafrost and polygonal net of ice wedges. In 10 years 4–5.5 m of permafrost have thawed and the flat surface has turned to badland

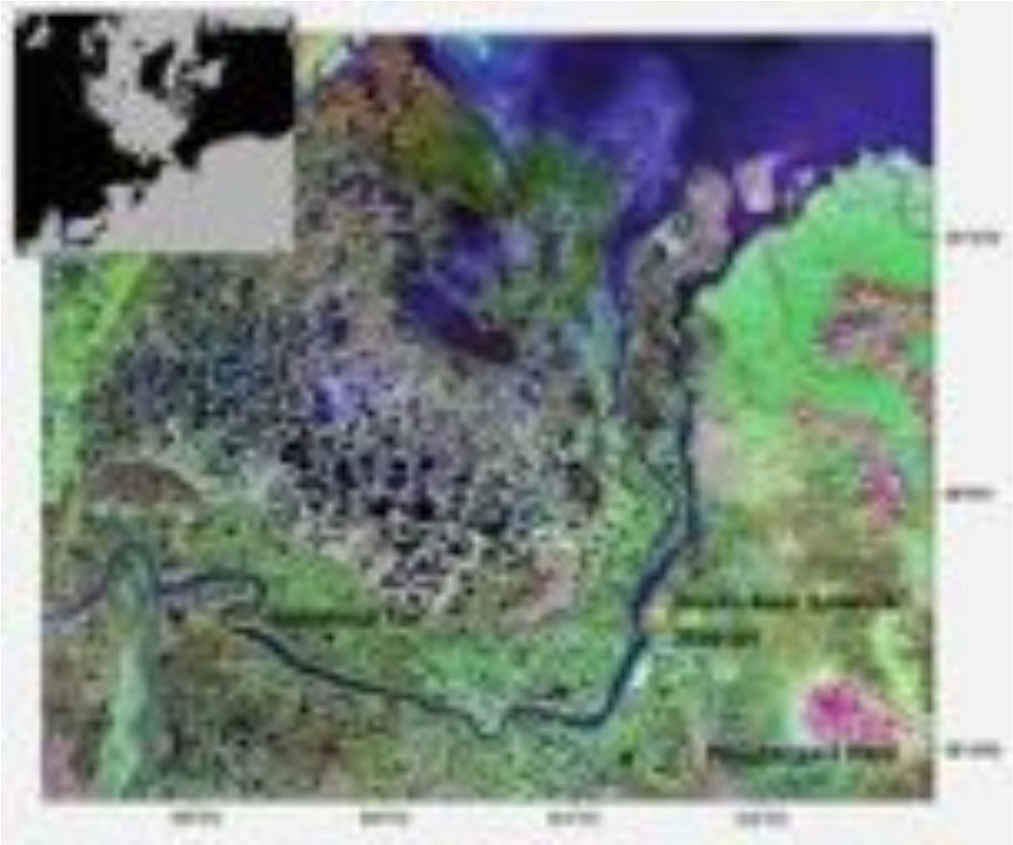

Fig. 10.3 Location of the North-East Science Station, Duvanii Yar and Pleistocene Park

this slope flowed down the Filipovka Tributary. This slope is only 0.1% of the watershed area but all the water in the Filipovka River turned into a mudflow.

The landscape shown in Fig. 10.2 is not unique. If ice wedges are covered with a thin layer of soil, then after a fire polygonal depressions appear. If, for example, the depth of the soil layer were only 0.7 m, and summer thaw depths increased to 1 m, then each year 0.3 m of ice would thaw. Previously this was a rather rare phenomenon. Now due to global warming it is becoming much more common in northern

Fig. 10.4 Gentle slope in the basin of Filipovka River, where the year before the image was taken, fire provoked permafrost degradation, and finally the entire soil layer has slid down to the river. In the next year herbs appeared (*yellow* color) on this slope and their roots have stopped the erosion

Siberia, and even in undisturbed places such reliefs can appear. And if the climate warms up by an additional 3°C, then the entire yedoma region would look like those in Figs. 10.1, 10.2, or 10.4.

10.3 Halting the Permafrost Thaw

Regional climate might be cooled via a change in landscape albedo. During summer dark green forests and shrubs absorb more heat compared to light green grasses and herbs (Foley et al. 1994; Lee et al. 2011). If dark forest and shrubs were removed, then from autumn to spring (8 months per year) northern landscapes would be white, reflecting the heat from the sun. This solution is extreme, and another solution exists. Soil surface is warmed in the summer and cooled in the winter. But at a depth of ~10 m there are no seasonal amplitudes of temperature, and it is roughly equal to the mean annual temperature of the soil's surface, which in turn depends on the mean temperature of the air. But this dependency is complicated. In the summer, soil temperature is roughly equal to air temperature, while in the winter a layer of snow exists between the soil and air, which is a good heat insulator. During such times air temperature can reach −50°C, while soil surface temperatures stay at −10°C. A decade ago the mean annual temperature near our station was −11°C. In the absence of snow the permafrost temperature would also be −11°C. But owing to the snow temperatures of permafrost are −6°C to −7°C. If we were to press this snow then it would lose most of its heat insulating abilities, and the permafrost would cool.

To artificially change vegetation and snow density on such a huge scale is near impossible. However it can happen naturally, through the trampling actions of large mammals, in particular herbivores. Currently, northern Siberia's mammalian biomass is too small for such trampling. However, as we argue below, this was not always the case.

10.4 Current Biodiversity in Northern Siberia

If one were to travel through the entirety of Siberia from south to north using winter roads, or drive on the boat along the Kolyma River (2,000 km) one would likely not meet any big animals. Using snowmobiles, boats, helicopters, we have travelled tens of thousands of kilometers along the Siberian north, and although looking carefully we have seen only eight bears, two wolves, two lynxes and one wolverine. It could be assumed that this territory is too severe to sustain many large mammals. But that is not true.

The East Siberian Sea is even more northerly and severe than Siberia. It is clear from ice only for 1–2 months of the year. However, when we boated on it, from the mouth of Kolyma River to Wrangel Island and back (roughly 1,600 km), we observed ~3,000 seals, ~300 walruses, 11 whale herds and 23 white bears. Admittedly these animals are not herbivores: they are positioned on the top of the trophic pyramid. However their total biomass, despite severe conditions, is several tons per km^2. Wrangel Island is the most severe wild nature reserve in Russia. Of the herbivores, only lemmings, as well as reindeers and musk ox reintroduced in twentieth century live there. However it is one of the richest Russian reserves based both on animal density and total biomass.

Northern Siberia has become a desert due to human action. In the seventeenth century when sable trappers reached Kolyma, up to 18,000 sables were trapped per year. At the same time snow geese were so abundant that tundra in the summer would appear to be covered with snow (Syroechkovskii 1986). However shortly after this both sable and snow goose disappeared completely. At the beginning of the nineteenth century, not far from our station each autumn around 100,000 wild reindeer crossed the Kolyma River (Syroechkovskii 1986). Today none of the locals remember this. For reindeer herders wild reindeer are major pests, and are actively killed, such that they have vanished from the area. Moose were rare in the region for a long time, but after the USSR collapse poaching control has been substantially reduced, and the populations of moose have declined ten-fold.

However the picture is not all bleak. Last century work was started on the reintroduction of sable. Current prices on sable fur can’t cover the expenses connected with trapping, and today on the Kolyma the sable population has recovered. Muskrats were also introduced to the Kolyma in the twentieth century, and now this species is widespread. On the Taimyr Peninsula, Wrangel Island, mouths of Lena, Indigirka and Kolyma Rivers, musk-ox were introduced and they have adapted everywhere and actively increased their populations. Due to economic reasons the Taimyr Peninsula lost its domestic reindeer herds, and a 100,000 domestic reindeer have been replaced with a million wild reindeers (Syroechkovskii 1986).

10.5 The Climatic Hypothesis and the Ecosystem Hypothesis

The current low density of animals in northern Siberia is not connected with severe climate. During glacial epochs the climate was more severe, yet mammoths, wooly rhinos, horses, bison, elk, musk-ox, antelopes (saiga), and cave lions thrived (Sher et al. 2005). During the Pleistocene the glacial mammoth steppe was the planet's biggest biome. It spanned from France to Canada and from Arctic Islands to China (Adams et al. 1990; Guthrie 1990). During interglacial warming forests took over, and the north of Siberia, Alaska and the Yukon Territory were refugia for this psychrophilic ecosystem. Trees and shrubs would also have penetrated to these places, but they were not the dominant vegetation cover (Sher 1997). It is only during the last interglacial, in the Holocene, that the mammoth steppe has vanished. Instead it has been replaced by moss forest and tundra. Many lakes and wetlands have appeared. It has been assumed that, during the Holocene, in contrast to other previous interglacials (Sher 1997), a cold dry steppe-like climate switched to a warmer wetter climate that, in turn, caused the disappearance of grasslands and their megafauna (Guthrie 1990; Vereshchagin and Tikhonov 1990; Velichko and Zelikson 2001; Schirrmeister et al. 2002; Sher et al. 2005). This is often referred to as the Climatic Hypothesis.

In contrast to the Climatic Hypothesis we propose an Ecosystem Hypothesis (Zimov and Chupryninm 1991; Zimov et al. 1995; Zimov 2005), which assumes that the mammoth ecosystem was relatively insensitive to climatic variation and that numerous animals maintained highly productive grasslands over a wide range of climates. Under such a strong disturbance regime, mosses and shrubs were trampled, and highly productive, actively transpiring graminoids and herbs dominated (Zimov and Chupryninm 1991; Zimov et al. 1995; Zimov 2005). During the PHT the rise in precipitation was accompanied by increased temperatures, so climatic aridity did not change substantially. The Ecosystem Hypothesis proposes: "In some places, such as sandy and stony ground, trees and shrubs would have appeared. This might have caused changes in the relative proportion of horses and moose. But overall, if climate was the only controlling factor, the total grassland productivity and the number of herbivores should have increased in the Holocene" (Zimov 2005, p. 798). We propose that the disappearance of the mammoth steppe was caused by an increase in hunting pressure. The resulting decline in abundance of animals would have reduced forage consumption, causing an accumulation of surface leaf litter, insulating the soil, and reducing summer soil temperatures. This would have initiated a cascade of other ecosystem changes, including a decline in productivity and transpiration, wetter soils, and lower nutrient availability. These, in turn, would have altered the competitive balance among species, promoting the growth of mosses and shrubs and reducing the abundance of grasses. The net effect would be a decline in forage quantity and quality, leading to continued decline in animal numbers (Zimov and Chupryninm 1991; Zimov et al. 1995; Zimov 2005). An important implication of the Ecosystem Hypothesis is that the grassland ecosystem could be regenerated in the north if one could increase the density and diversity of animals.

10.6 Chronological Support for the Ecosystem Hypothesis

Recent publication of many new ^{14}C dates of animal fossils from Alaska and Yukon provide an opportunity to clarify the relative chronologies of animal extinction, vegetation dynamics, and human colonization (Guthrie 2006). In this section we compare these data with chronologies assumed by the Ecosystem and Climatic Hypotheses. We presented the data in a form of probability distribution (each ^{14}C data is presented as a bell-curve with a 400 year base). The total ^{14}C data density curve is sum of area of all the bell-curves (Fig. 10.5).

Greenland ice cores show abrupt temperature and precipitation fluctuations at the PHT. At 14,650 calendar years BP (approximately 12,500 ^{14}C years BP (Reimer et al. 2004)) the average Greenland temperature rose sharply (up to Holocene levels), and precipitation doubled (the Bolling Warming Event (BWE)). During the Younger Dryas (11,600–12,800 calendar years BP) climatic parameters returned to their initial state, and at the end of the Younger Dryas temperatures rose sharply again (Severinghaus and Brook 1999). Similar climatic dynamics were recorded at both high and low latitudes of the northern hemisphere (Severinghaus and Brook 1999), and similar dynamics should also be recorded for Alaska.

If the Climatic Hypothesis explained vegetation and animal dynamics, steppe-like vegetation would have been replaced by tundra vegetation during the BWE, and the steppe would have been reestablished during the Younger Dryas, when the climate returned to glacial conditions. We propose that in fact, the opposite happened. Glacial climate was not favorable for the mammoth steppe ecosystem in Alaska and the Yukon, and during the LGM nine animal species went extinct (Guthrie 2006). When the climate warmed from 15,000 to 12,400 radiocarbon years BP there was a substantial rise in abundance of grasses and sedges, and animal densities increased (Fig. 10.5). Pollen influx of *Artemisia*, a drought-adapted species, rose even more than the influx of other species. This suggests that aridity did not decrease at the PHT.

The BWE did not affect plant species composition but affected animals. Data on Fig. 10.5 indicates that strong warming and increases of snow depth during the BWE was not accompanied by the extinction of any species. On the contrary animal populations grew. During glaciations the elk (*Cervus*) population was very small (only two ^{14}C dates (Guthrie 2006)). This population increased sharply by ~12,600 ^{14}C years BP. The Elk peak is statistically the most reliable (50 dates). Its right slope is very steep. The ^{14}C dating represented by this slope has a standard deviation of ± 90–240 years (Guthrie 2006). We did additional smoothing (± 200 year) in building the figures of ^{14}C date density. Thus in reality this slope is almost vertical- there was a sharp population rise. Reintroduction of musk-ox to Wrangel Island is a contemporary example of such a rise. Their population grew 100 times in 35 years (Vartanyan 2007).

Approximately 12,400 years ago an abrupt change occurred: horses vanished, bison disappeared for over 300 years, and mammoth and elk populations began to decrease sharply (Fig. 10.5). It is clear that this abrupt faunal change was not triggered

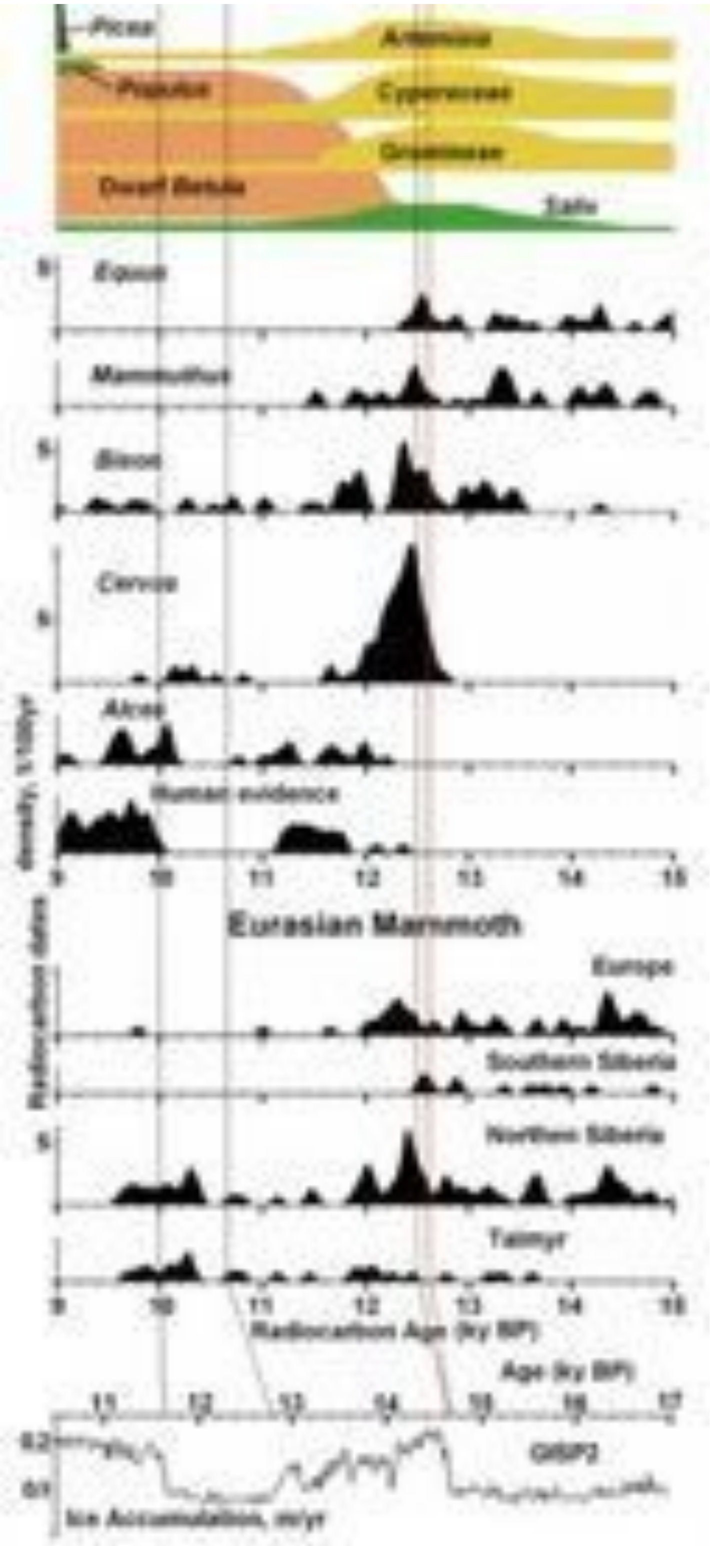

Fig. 10.5 *Upper part*: generalized pollen record, density of ^{14}C dates of animals, and human evidence for Alaska and Yukon (from Guthrie 2006). *Lower part*: density of ^{14}C dates of mammoths for Europe, southern Siberia and China (Vasil'chuk et al. 1997; Kuzmin et al. 2001), the entire Siberian Arctic (Vasil'chuk et al. 1997; Kuzmin et al. 2001; Sher et al. 2005), and the

by vegetation change, because vegetation was stable during this period. The only thing corresponding with these massive extinctions was the first evidence of humans (12,370 ^{14}C years BP) (Fig. 10.5). It therefore appears plausible that a relatively small number of hunters triggered the collapse of several herbivore populations (Martin 1984).

After the first appearance of humans, some of the species recovered their populations (which is in accord with mathematical modeling results (Alroy 2001)), but human population continued to increase and this led to herbivores' extinction. It was only well after that that pastures degraded and dwarf *Betula* appeared. The appearance of moose (*Alces)* at 12,200 radiocarbon years BP closely corresponds with a decrease in *Salix* and rise in dwarf *Betula*, which is not the usual forage for the moose. One possible explanation for this shift is that, as long as there were abundant bison, elk, and mammoth, which actively ate willow sprouts, willow shrubs would not have grown above the snow cover. Moose (tallest hoofed animal) may have appeared in large numbers only when populations of other animals had decreased, creating a new feeding niche–tall willow shrubs.

The increase in ^{14}C dates of mammoths at the BWE (Fig. 10.5) can also be observed in Europe and the Siberian north (Vasil'chuk et al. 1997; Sher et al. 2005). During the Holocene the mammoth population on Wrangel Island increased substantially. There were five-fold more Holocene dates there (3,730–7,710 years BP range) than Pleistocene dates (Vartanyan 2007). This occurred despite the fact that, in contrast to Alaska where loess accumulated throughout the Holocene (Muhs 2003), in Siberia sedimentation stopped (Schirrmeister et al. 2002; Sher et al. 2005), and most of the bones remained on the surface, where weathering would have destroyed them.

10.7 The Mammoth Steppe Climatic Envelope

The essence of the Climatic Hypothesis is as follows: mammoths, other extinct animals, and their pastures (i.e., the mammoth steppe) required a certain range of climatic parameters that defined their climatic envelope. In the Holocene, climate changed radically, and territories with suitable climate for the mammoth steppe disappeared throughout the planet. To further assess the Climatic Hypothesis, we define the mammoth steppe climatic envelope, i.e., the optimal and peripheral climatic space of the mammoth steppe.

Here we discuss two climatic characteristics – heat and moisture, as aridity level is determined by these two factors. We characterize moisture by annual precipitation (P) and heat by annual radiation balance (R), which correlates closely with mean summer temperature. We consider a two-dimensional climate space with

Fig. 10.5 (continued) Taimyr Peninsula (Sher et al. 2005); snow accumulation for Greenland (Severinghaus and Brook 1999). *Vertical black lines* represent Younger Dryas boundaries based on IntCal04 (Reimer et al. 2004); the *red line* is a corrected (elk peak correction) Bowling radiocarbon boundary

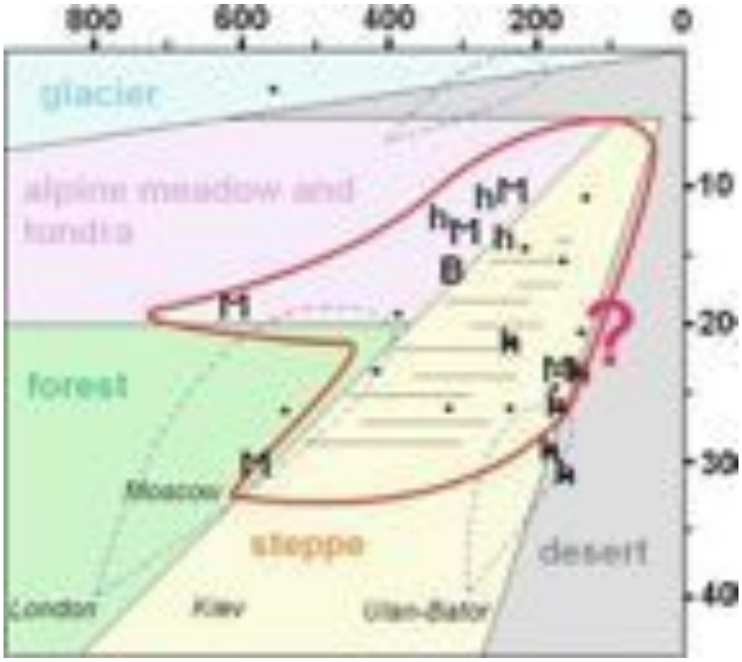

Fig. 10.6 Climatic space with the most important landscape boundaries shown. The axis R could also represent average summer temperatures (20 kkal/cm^2/year approximately corresponds to 10°C). *Black dots* are the meteorological stations of northeast Siberia (see Fig. 10.7). *h* represents Holocene and modern horse grasslands in Siberia; *M* and *B* are Holocene grasslands of mammoths and Siberian bison. *Brown cross-hatching lines* represent Holocene natural bison habitat of interior Alaska and northwestern Canada. Question mark (‘?’) is the presumed locations of the mammoth steppe climatic envelope that are consistent with the Climatic Hypothesis. The *red solid line* is our estimate of the boundary of the continuous climatic envelope of mammoth steppe. *Dashed blue lines* enclose areas where climatic trajectories lie, during the last glacial cycle, in three geographical locations: London, Ulan-Bator and top of the 1,700 m mountains near the Oymyakon region. Today’s snow line of the Oymyakon Mountains is situated on 2,300 m

these two parameters (coordinates). Aridity can be assessed using Budyko’s radiation aridity index (Budyko 1984), which is the ratio of R (in this case energy received by the landscape) to the energy needed to evaporate an amount of water equal to P. If this index is less than 1, the climate is humid; if greater than 1, the climate is arid: with values between 1 and 2 equivalent to steppe, 2–3 semi-desert, and >3 desert environments (Budyko 1984).

Such a two-dimensional climate space is illustrated in Fig. 10.6, which shows the most important boundaries for desert, arid and humid climates (Budyko 1984). Beside those we show the approximate position of three additional boundaries: the snow line where R equals the energy needed to melt an amount of ice equivalent to annual precipitation; the northern (altitudinal) forest border; and the boundary of polar desert. Vertical movement in this climate space is equivalent to latitudinal movement in real (geographical) space. Movement to the right of this climate space is equivalent to movement from the ocean to the continental interior. Movement to the upper left quadrant is equivalent to moving upward in elevation: colder with more precipitation.

On the basis of this envelope, we make five arguments: (1) Similar to geographical space, in climatic space the mammoth ecosystem should have an optimal zone and a peripheral zone where conditions for survival are severe; (2) The mammoth steppe existed in different climates on a huge territory for a long period of time. Mammoths lived simultaneously in Spain, England, Mongolia, China and Arctic Islands (Vasil'chuk et al. 1997; Kuzmin et al. 2001; Sher et al. 2005; Alvarez-Lao and García 2011). It is obvious that climate differed between these regions, therefore, it can be assumed that the mammoth steppe climatic area was spacious; (3) If mammoths became extinct in the Holocene everywhere because of climate then there is currently no place on the planet where the climate would still be suitable for the mammoths. It then follows from the Climatic Hypothesis that mammoths were living under a unique combination of R and P, which are not met anywhere today; (4) It seems that the mammoth steppe optimum must be situated in the colder part of the steppe sector (Fig. 10.6), and their range should move smoothly into temperate climate steppe; (5) The range of climatic optimum for mammoth steppe was approximately 150–300 mm of precipitation and 8–10°C summer temperatures, which corresponds to climatic reconstructions for Eastern Europe, where the mammoth ecosystem received 250–300 mm of precipitation annually (Velichko and Zelikson 2001).

In the PHT the previously arid climate in the north of Siberia did not become humid (Zimov and Chupryninm 1991; Zimov et al. 1995). Figure 10.7 shows the meteorological stations of northeastern Siberia, where radiation balance observations are conducted (all circumpolar, including islands and continental); these are also shown on Fig. 10.6 with black points. We see that even though this region has abundant lakes and wetlands its climate is arid. The most arid part is in the Pole of Cold in Oymyakon (Budyko's index = 3.28; the most right and lowest black dot on Fig.10.6), and most humid is in mountains near the glacier, not far from Oymyakon (Budyko's index = 0.1; the most upper and left dot). We can use another known climatic index, in which potential evaporation is calculated by summer temperatures, but we get the same results – the climate is arid (Sokolov and Konyushkov 1998). Around 400–500 mm of precipitation evaporates from lake surfaces or high productive grasslands in these territories; this is twice precipitation this region receives (Zimov and Chupryninm 1991; Zimov et al. 1995). Lakes persist only because of drainage from slowly transpiring forests and tundra. In Central Yakutia vast steppe territories grazed by horses do not have any river drainage (Pavlov 1984). Nevertheless, proponents of the Climatic Hypothesis suggest that the climate of northeast Siberia and Alaska is too wet for the mammoth steppe (Guthrie 1990; Vereshchagin and Tikhonov 1990; Velichko and Zelikson 2001; Sher et al. 2005). If correct, the climatic envelope of the mammoth steppe would be restricted to a small area between the upland cold deserts of Tibet and the polar deserts of the Canadian Arctic (indicated with a red question mark in Fig. 10.6). The Climatic Hypothesis assumes that this small envelope occupied a huge territory of Eurasia and Northern America during both the LGM and the BWE. This climate space was

Fig. 10.7 Budyko's radiation aridity index in different locations North-Eastern Siberia

characterized by only ~100 mm of precipitation, raising questions of how the glaciers of Europe could have developed and persisted.

The last mammoth refuge on the continent was the north of Taimyr Peninsula, where they persisted until the Holocene (Sher et al. 2005). If the Climatic Hypothesis holds, then the entire climatic envelope of mammoths should be situated in even more severe conditions than on the Taimyr Peninsula (polar desert). However mammoths lived in the Iberian Peninsula (Alvarez-Lao and García 2011), which would suggest that summer there (40°N) was colder than in Taimyr today (i.e., 25–30°C colder than today). This is not possible. We suggest that the Climatic Hypothesis as currently stated (i.e., "colder and dryer") is unrealizable. The mammoth steppe could exist at 100 mm precipitation and with northern Taimyr summer temperatures, but it's unlikely that this represented optimal conditions.

It is possible to amend the Climatic Hypothesis by assuming that R and P changed very quickly, and that every region had its own subspecies of mammoth that were adapted to local conditions. Hence mammoths wouldn't have had time to adapt to fluctuations or migrate to more suitable regions. However this would not explain why in Europe, Northern Siberia and North America mammoths sustained bigger climatic jumps yet vanished under relatively stable climate (see Fig. 10.5). A better explanation is that the mammoth steppe did not disappear due to climate.

10.8 Climatic Envelope of Mammals of the Mammoth Steppe Ecosystem

In this section we revisit the numerous radiocarbon dates for bones of animals that used to live in the mammoth steppe ecosystem. Many of these bones date from the Holocene and therefore experienced a climate similar to the modern climate. By looking on climatic maps at the modern climate (R and P) of these locations, we can directly estimate the climate experienced by Holocene populations of these species. These points in climate space are shown in Fig. 10.6.

The lack of horses in Alaska during the Holocene has been lead to suggestions that the modern Alaskan climate is not suitable for them (Guthrie 2006). However, in Siberia, where the climate is similar, horses persisted well into the Holocene (up to 2,200 ^{14}C years BP) in the arid far north (Lena delta and New Siberian Islands) and in humid climates (the Taimyr) (Sher et al. 2005). The semi-wild Yakutian horses today occupy a more southern and warmer climate (Fig. 10.6).

With bison, the situation is the reverse, with only one Holocene bison date in northern Siberia (9,300 ^{14}C years BP) (Sher et al. 2005), but extensive bison distributions in interior Alaska and the Yukon throughout most of the Holocene. They occurred along the arctic coast as far north as Victoria Island and as far south as southern Alaska near Anchorage (Stephenson et al. 2001). The climatic envelope of the American bison is shown in Fig. 10.6 with a dotted line.

Reindeer now live on the far north and in Mongolia. In historical times their southern boundary passed through Germany along the steppes of Eastern Europe (Syroechkovskii 1986). Therefore the climatic envelope of reindeer occupies almost the entire climate space of Fig. 10.6. In many regions of Siberia and North America musk-ox have lived until historical time (Sher et al. 2005), and as a result of recent reintroductions they currently live in Norway, Siberia, and Alaska.

We have no Holocene dates for the wooly rhinoceros, but their bones tend to occur in regions that are more arid than those of mammoths. For example, the northwestern portion of Eurasia to the north of 62°N including Taimyr is a humid part of the mammoth steppe. Many mammoth remains were found there but no rhinos (Garrut and Boeskorov 2001). On the other hand, wooly rhinos were common in the most arid regions of mammoth steppe, south of Central Siberia and Mongolia (Garrut and Boeskorov 2001), where mammoths are rare (Kuzmin et al. 2001).

Mammoths existed in the arid zone in the Holocene (Wrangel Island (Fig. 10.8), with the most recent date of 3,730 ^{14}C years BP) (Vartanyan 2007), in the humid zone on the north of Western Siberia (Gydan peninsula, 9,730 ^{14}C years BP), in the northern Taimyr (9,670 ^{14}C years BP) (Sher et al. 2005), in the very humid St. Paul Island in the Bering Sea (5,700 ^{14}C years BP) (Yesner et al. 2007; Guthrie 2004), and on the coast of Gulf of Finland (9,780 ^{14}C years BP) (Vasil'chuk et al. 1997). While the early Holocene climate may not have been the same as today; it is indisputable that on Wrangel Island and on St. Paulo Island mammoth lived in a late Holocene climate.

On the climatic space (Fig. 10.6) these sites are situated very far from each other. Wrangel Island is a dry polar desert, and St. Paulo has a very humid climate with no

Fig. 10.8 Wrangel Island was the last mammoth refugium. This picture shows grassland near the Ushakovskaya weather station, where the average July temperature is 1°C. The territory is characterized by high animal nitrogen inputs. It is the middle of September, but photosynthesis continues

permafrost. And the fact that mammoth lived on these two islands genetically isolated for the long time suggests that the mammoth's climatic envelope was very wide.

The ^{14}C data indicated that during the LGM mammoths lived on the climatically severe archipelago of New Siberia (79–80°N) (Sher et al. 2005) and Wrangel Island (Vartanyan 2007). They continued to live there in the Holocene. Today summer temperatures on these islands are approximately 0°C, and the vegetation would not feed a mammoth population. The paradox is that under the current climate, the same place can be a polar desert (in the absence of animals) or grassland (if animals are present). During the last 50 years, after the reintroduction of herbivores on Wrangel Island, ungulate biomass has exceeded the intended density (calculated maximum) by almost an order of magnitude (Vartanyan 2007). We suggest this happened because the biomass of forage has increased as herbivores maintain their grasslands. This is only the beginning of ecosystem succession. The potential grassland productivity on the island is shown in Fig. 10.7. Biological productivity in the north is limited less by photosynthesis than by nutrients (Chapin et al. 1995). Nutrient cycling is limited by slow decomposition and nutrient release from soil organic matter. Only in the warm stomachs of animals can this process be substantially accelerated.

In summary, the animals of the mammoth steppe occupied a broad climatic envelope. Similarly the distribution of modern tundra does not depend on aridity but occurs in sites ranging from 50 to 1,000 mm of annual precipitation. Based on the above information, we tried to reconstruct the boundary for a continuous climatic envelope for the mammoth steppe (Fig. 10.7). In geographical areas that now lie inside the envelope, the mammoth steppe ecosystem would not vanish because of R and P changes during PHT. The next important question is whether animal population densities in the mammoth steppe were high enough to prevent expansion of moss, shrubs, and trees.

10.9 Mammalian Population Density of the Mammoth Steppe

Animal density for the mammoth steppe can be estimated from the number of bones found in permafrost. However, from most of the skeletons, few to no bones are preserved (Guthrie 1990; Sher et al. 2005). We have reconstructed animal densities using several methods for different sites. We have done this most precisely based on data collected at Duvanii Yar in the Kolyma River lowland (68°38′N, 159°07′E), the largest yedoma exposure (Vasil'chuk et al. 2001; Zimov et al. 2006b) (Fig. 10.1). During the time of yedoma accumulation, this territory, remote from mountains and hills, was a flat plain, and animal density in the area was likely determined by forage availability.

The bone concentration in the Duvanii Yar yedoma (as for most other yedoma and loess) is small, only one bone (or its fragment) for each ~500 m^3, therefore it is difficult to find bones on the cliffs (exposure). However accounting for the 50 m height of exposure, the density of bones is 1 bone per 10 m^2 or 100,000 bones per km^2. Observing this high density is only possible on the exposed shores, where sediments slide or crumble and are washed from the area by waves and streams. Well-washed bands several meters wide appear on the Duvanii Yar only rarely. After a storm the water level in the rivers drops abruptly, and mud flowing down the exposures don't have enough time to cover all exposed (washed) bones. For minor rivers, where there are no big waves, large exposures and beaches are absent.

Bones are initially deposited at the location of an animal's death. Predators can disperse some of the bones, although this is unlikely for the tusks and molars of mammoths. On the large beaches at Duvanii Yar mammoth bones occur in groups several tens of meters from one another and belong to one animal (one skeleton), making it possible to directly calculate the density of mammoth skeletons. On average, each accumulation is 8–10 bones (up to 19). Fragments of tusks and/or molars are present in most of the accumulations (Fig. 10.9). On three occasions (1998, 2009 and 2011) the beach was well washed and we were able to count the density of mammoth skeletons on four transects. Densities were 1,030, 1,170, 1,380 and 1,450 per km^2. This density was calculated as the number of bone accumulation centers falling into the bands of well-washed shore (width of the bands multiplied by length) (Zimov et al. under review).

The number of tusks can also be used to calculate the density of mammoth skeletons in the yedoma. Average annual commercial collections of mammoth tusks from Duvanii Yar are about 250 kg/year, and range from 70 to 450 kg/year. Due to the length of the exposure (10 km) and the rate of erosion (2.5 m/year), the density of the tusks is equal to 10 t/km^2. The average weight of a tusk in this region is 25 kg (39 kg for males and 11 kg for females) (Vereshchagin and Tikhonov 1990). Thus, the density of commercial tusks is 400/km^2. However most of the tusks are disintegrated by being on the surface and in the yedoma are preserved only as small fragments without commercial value. If we assume that only 20% of tusks (by weight of all tusks) are preserved in permafrost and appear in the collection, then we obtain 1,000 skeletons/km^2, the same mammoth density that we calculated from skeleton density at Duvanii Yar.

In order to obtain a precise estimate of hoofed animal density, we used full bone collections gathered in 2007 and in 2009 over the area of ~0.01 km^2. The collection is shown in Fig. 10.10. Not shown are 23 woolly rhinoceros bones (that were found in 6 accumulations), 4 musk-ox bones, 3 elk bones, 2 moose bones, 1 hare bone, 4 wolf bones, 2 cave lion bones, and 61 unidentified mammoth bone fragments. The distribution of fossils from different species on Duvanii Yar was very similar to the distribution of bones obtained from the ~3,000 bones collected in the entire region

Fig. 10.9 August 2011 in the central part of the Duvanii Yar. Width of the well-washed band in the central part of the shore was on average 6–10 m. Here, in 1,570 m transect, 169 bones and bones fragments of mammoths were found: 5 bones were isolated, 4 accumulations with 2 bones, and 32 accumulations with 3–10 bones or their fragments. In 29 accumulations particles of molars and tusks were present. The diameter of each accumulation is ~10 m. In this image we show all four accumulations with mammoth jaws

of northern Siberia (Sher et al. 2005). So the species distribution on Duvanii Yar is typical of the Siberian north. Massive bones dominate for each species (Fig. 10.10) with thin bones, for example ribs, being very rare, and the smallest bones absent.

To compare the skeletal densities of different species, we used the dependence (proportion) of the relative probability of bones to persist (to be found) to bone weight. To correct for the influence of bone shape (length), we used a reduced weight (bone weight (g)/bone length (cm)$^{3/2}$). Linear dependence was recorded for all species and holds true for a range of bone weights from grams to kilograms (Fig. 10.11). The same dependency (linear) was recorded for the mammoth collection gathered from the entire Siberian north (Fig. 10.11). The number of bones in the collection is also proportional to the number of dead animals. Assuming that all four graphs reflect the same functional dependence on bone weight, we determined a relative density of skeletons for four species (using the ratio between equation coefficients (Fig. 10.11)). We determined (rounding) that bison skeletons were 20 times more abundant than mammoth skeletons, horses 30 times and reindeer 80 times. These estimates are close to those obtained by using the average number of bones in the accumulations (Zimov et al. under review).

Fig. 10.10 Bones of mammoths, horses, bison and reindeers collected on the shore of Kolyma river on the western part of Duvanii Yar exposure on the area of ~1 ha. Bones are positioned to be consistent with their anatomical position. Mewed reindeer horns presented separately

Duvanii Yar loess accumulated from 42,000 to 13,000 years BP (there are 40 ^{14}C dates from this exposure (Vasil'chuk et al. 2001)). In collections gathered from northern Siberia, ~10% of all of the mammoth bones were older than 45,000 years (Sher et al. 2005). Therefore, we took a more conservative estimate that all bones accumulated for ~40,000 years. The average age for a dead mammoth, calculated based on annual rings on tusks, was 40 years (maximum age ~80 years) (Vereshchagin and Tikhonov 1990). We are making a conservative evaluation of the density of dead mammoths at 1,000/km^2. From this we determined that the average adult mammoth density was about 1/km^2.

There were very few bones of young ungulate animals; they are relatively soft and therefore are often eaten by predators. By accounting for high predator pressure, and the maximum age of modern animals, we assumed that the average longevity of mature horses, bison, and lions was 10 years, 7 years for reindeer, and 5 years for wolves, which gave us an average animal density per square kilometre of 5 bison (total weight of 3 t), 7.5 horses (3 t), 15 reindeer (1.5 t), 0.25

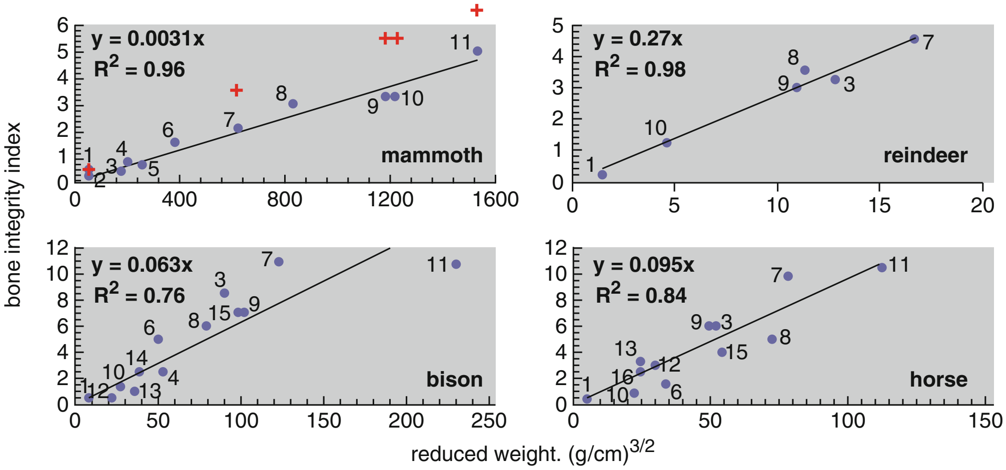

Fig. 10.11 Dependency of bone integrity on reduced weight. Bone integrity index is the ratio of the number of bones of a specific type in a collection (Fig. 10.10) to the number of such bones in an entire skeleton of a species. 1 – rib; 2 – caudal vertebra; 3 – metapodial; 4 – carpal and tarsal; 5 – vertebra; 6 – calcanea; 7 – radius and tibia**;** 8 – mandible; 9 – scapula and pelvis; 10 – molar; 11 – humerus and femur; 12 – phalanx I; 13 – phalanx II; 14 – ulna; 15 – talus; 16 – phalanx III (hoof). *Red* "+" – data from big mammoth ^{14}C collection gathered in all of Siberia (Sher et al. 2005)

lions (0.05 t), and 1 wolf (0.05 t). By adding the weight of the mammoths (=2.5 t (Vereshchagin and Tikhonov 1990)) to the rest of the more uncommon herbivores (0.5 t), we calculated a total herbivore biomass of 10.5 t, enough to feed wolves. All of these estimates were averaged over a period of 40,000 years. Mammoth density dynamics are illustrated on Fig. 10.12 (Kuzmin et al. 2001; Sher et al. 2005; Vartanyan 2007; Nikolskiy et al. 2009). During the LGM, the number of mammoths was at their lowest; it increased as the climate became warmer.

Similarly, we obtained equivalent estimates of animal density for the Lena river delta, New Siberian and St. Paulo Islands (Zimov et al. under review). These estimates are approximate. Many parameters (animals weight, shore width, etc.) were rounded, but the accuracy of these estimates is probably similar to the accuracy of the estimates of animal densities in modern ecosystems. Our roughest estimate was for predators, but considering that almost all of the vertebrae of horses were eaten, and that predator action broke all of the humeral bones, we believe that the predator population was large enough to eat most things.

We also see large number of herbivores in the north today. Semi-wild horses inhabit northern Siberia. Their biomass in Yakutia exceeds the biomass of reindeer (Agricultural Atlas of Yakutia 1989). The modern density of wild and semi-wild reindeer in the forest and tundra of the north-eastern Siberia is only 60 kg/km^2 (1 per km^2 (Agricultural Atlas of Yakutia 1989)). In contrast, the current biomass for horses in the Aleko-Kuel region, (300 km west of Duvanii Yar) on the most productive low-lying meadow, is 200 times this value (30 horses/km^2), which is close to the above estimate of 10.5 t. The same density of ungulate animals is maintained on the grasslands of Pleistocene Park (100 km of east of Duvanii Yar) (Fig. 10.13).

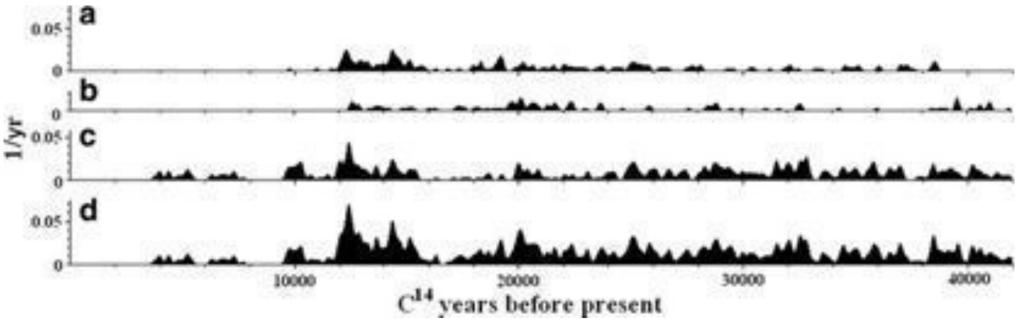

Fig. 10.12 Density of ^{14}C dates of Siberian mammoths

Fig. 10.13 Horses, bison and musk-ox inhabit Pleistocene Park. There are also three species of deer. This represents the highest diversity this area has seen in the last 12,000 years

10.10 Mammoth Steppe Physiology

Although the accuracy of any single calculation might be questioned, as with any paleo-reconstruction, the consistency of patterns that we obtained from many independent data sources and approaches suggest that the following inter-related conclusions are robust:

1. Plant, herbivore, and predator productivity in mammoth steppe was close to the theoretical maximum for a northern ecosystem. The ecosystem very efficiently utilized all resources. The density of animals and their community structure was similar to that of an African savanna. To feed animals, plants utilized all available water.
2. Vegetation was dominated by palatable high-productivity grasses, herbs and willow shrubs (Guthrie 1990; Sher et al. 2005). No other vegetation could maintain 10 t/km^2 of herbivore biomass.

Fig. 10.14 Part of the Duvanii Yar exposure. The soils (yedoma) are fertile, so even though it's a cold northern-faced slope, highly productive grasses appear in locations of permafrost erosion. In this part of the exposure, grasses prevent erosion through root reinforcement of the soil. In conditions of cold and dry climate with herbivores absent, thermally insulating litter accumulates on the surface, fertility declines, and in several years grass productivity also declines. If herbivores appear on the site they maintain meadow productivity and also decrease permafrost thawing

3. The soils were fertile. The content of bio-available phosphorus in the yedoma is an order higher than in modern soils (Zhigotsky 1982). If soils of the mammoth steppe appear on the surface due to erosion, they are immediately overgrown by highly productive grasses and herbs (Fig. 10.14).
4. Winters were much longer than summers, and winter forage was a limiting resource. Therefore, summer overgrazing was not possible. In the summer animals could eat only half of all available forage. During winter herbivores ate all the rest (Fig. 10.15); however, without long-term damage to the grass community, since all living parts are preserved in the soil. Therefore, all of the insulated snow cover was trampled, and the soils cooled significantly during winter. A change in snow depth of ~10 cm changes the temperature of the permafrost by 1°C (Yershov 1998). Soils were fully trampled throughout the year, preventing the establishment of a moss layer and the expansion of slowly growing shrubs and trees into grasslands (Zimov et al. 1995). The albedo of the mammoth steppe was significantly higher than the albedo of forests and shrublands, especially during the snow season (Foley et al. 1994). Litter did not accumulate in the ecosystem. Therefore, at the beginning of the summer, until new grass had grown bare soil surface (Fig. 10.15) was intensively heated by the sun.
5. Moderate summer grazing stimulated the regrowth of grasses. As a result, grasses had no time to finish their life cycle and were covered with snow still having a high nutritional value. Plant species assemblage is usually determined from pollen records that are collected from loess strata. These records often consist of species that are not common in grasslands (Guthrie 1990;

Fig. 10.15 Pleistocene Park in spring after snowmelt. Ten years prior, the area was a continuous community of 2–3 m tall willow shrubs. Due to erosion and long-term active grazing, the plot developed into a meadow with fertile soils and nutritious grasses. Herbivores therefore graze in this area several times per winter, trample down snow, and eat all the vegetation that grows during the summer. The winter temperature of the soil surface at this site is 15–20°C colder than for grasslands without grazing. We presume that during herbivore population peaks in spring all of the mammoth steppe grasslands looked similar to this

Sher et al. 2005). If on some territory several meters of loess accumulated, it would indicate that another territory with sparse vegetation cover and strong winds would erode the same amount of dust, and that all of the spores and pollen (and everything aerodynamically lighter than sand including insect remains) from deflated areas would appear in pollen-poor grasslands and, in the end, in loess strata. These inferences can be applied to all mammoth steppes that formed on loess-dominated soils. In areas with poor stony or sandy soils, the productivity of palatable plants would be smaller and grazing and trampling would be weaker. Therefore, slow-growing unproductive plants were able to survive and persisted in the regional flora. Mammoth steppe biomes consist of different ecosystems: unproductive deflation areas, productive grasslands on loess or loamy soils, and tundra and forests (savanna) on poor soils. These patterns explain the complicated composition of the pollen spectrum.

6. Due to high productivity and corresponding plant transpiration, water was often a limiting resource; grass roots competing for water penetrated the entire depth of the active layer. This is additionally suggested by the fact that in the yedoma numerous thin grass roots are preserved (Sher et al. 2005). Near the permafrost table soils were thawed just for few weeks per year, and temperatures never rose substantially above zero, therefore organic decomposition was low, and labile carbon accumulated (Zimov et al. 2009). Hence the mammoth steppe was an ecosystem with a high rate of decomposition for aboveground biomass (in animals' stomachs), and a very low rate of decomposition in deeper soils.

7. The similarity of density and the assemblage of species on the northern and southern parts of the lowlands suggest that regular massive migrations of herbivores with regional differences in mortality were unlikely.
8. Mammoth steppe would only be stable under conditions of very high animal densities, as they had a strong impact on the environment. An expansion of the high-albedo psychrophilic steppe biome, whose dry soils and permafrost accumulate carbon (Zimov et al. 2006a, b; Zimov et al. 2009) and do not produce methane (Rivkina et al. 2006), would promote climate cooling and permafrost expansion, whereas a degradation of the ecosystem and permafrost in response to recent warming would amplify climate warming (Zimov and Zimov under review).
9. Mammoth steppe on the Siberian north was the coldest and driest part of the biome. In other grassland ecosystems, where there was 2–4 times more precipitation, and grass and herb productivity and animal densities were correspondingly higher. An analysis of paleovegetation maps indicates that during the LGM forested areas were 10 times smaller than in the Holocene, and that an area of grass-herb dominated ecosystem reached 70×10^6 km^2 (Adams and Faure 1998). If similar animals to the mammoth steppe consumed all forage, assuming average herbivore density of 20 t/km^2 (twice more than in the north of Siberia), we obtain global animal biomass values (1.4 billion tons) close to that obtained via methane emission by herbivores (Zimov and Zimov under review). During the LGM, wetlands were rare. For that period no ^{14}C basal peat initiation dates are know. They appeared in abundance only in the Holocene (Yu et al. 2010). Furthermore, during the LGM methane concentration in the atmosphere was almost half of Holocene values, and herbivores were the main source of methane due to a total herbivore biomass exceeding total modern biomass of humans and domestic animals combined (Zimov and Zimov under review). In the Holocene the density of herbivores declined by an order of magnitude (Zimov and Zimov under review).

10.11 The Pasture Ecosystem

During glacial periods ecosystems were different from that found today. Among plants grasses and herbs dominated. The main characteristic of grassland ecosystems was the abundance of herbivores, which maintained wet or dry pastures. In the spring these ecosystems looked like those on Fig. 10.15. Only bones and excrements were left on the surface. We propose to call these ecosystems pasture or grazing ecosystems. With the help of herbivores pasture ecosystems were dominant and could compete with forests even in humid climates.

On a geological timescale pasture ecosystems are amongst the youngest. These ecosystems have the highest rates of biocycling, with some of the most fertile soils. Unlike evergreen plants, fast growing grasses encourage grazing and trampling as it stimulates their growth. Grasses do not spend energy on toxins and thorns, and they maximise sunlight and water resources. The grazer's niche in this ecosystem is to eat everything that has grown during summer (rain season) and return all the nutrition back to soil through defecation. Predators in this ecosystem maintain herbivore population densities.

On different continents pasture ecosystems have different biological species, but similar assemblages of functional types. For example, the African antelopes and the cervids of Eurasia occupy similar functional types in pasture ecosystems. Pasture ecosystems are very dynamic: where forests or mossy tundra may need many years to recover after natural disasters (e.g., fires), pasture ecosystems may recover in several weeks. Over the course of the last million years, under the dynamic Pleistocene climate, the mammoth steppe and other pasture ecosystems replaced forests and occupied large parts of the world.

10.12 The Mammoth Steppe Ecosystem and Humans

Mathematical modelling indicates that for the current climate in north-eastern Siberia, two stable states of nature exist: in the presence of strong hunting pressure mossy-shrub plant communities exist, while in the absence of hunting pressure grass dominated communities prevail (Zimov and Chupryninm 1991; Zimov et al. 1995). To shift environment from one state to another, there is no need to exterminate all animals. However, in the north of Siberia little evidence of humans during the PHT exists, and in Russia the overkill hypothesis (Martin 1984) is not popular. We have shown that there were around 100 million large animals living in the north. In Africa and Asia humans did not exterminate the megafauna (Barnosky et al. 2004; Louys 2008). Why then did this happen in the north with mammoths? We can't provide definitive proof that humans drove the mammoths extinct. However we can show that humans could do it, both physically and mentally. And we show that the density of artefacts in the north does not contradiction that.

Initially *Homo sapiens* appeared in the southern part of the mammoth steppe and for many thousands of years was part of that ecosystem. Animals were so abundant in the mammoth steppe that humans would not need to look for animals. However, many of the animals were dangerous. Humans were the slowest species with the most defenseless young. Biologically, humans are least adapted to cold and long winters. Therefore, the survival of humans and possibilities for expansion into the vast woodless plains of the north were not limited by animal density, but by severe climate conditions, the absence of natural shelters, and their level of technology. Every new dwelling type, weapons, clothes, and fire-making techniques all contributed to increased human efficiency and survival, and therefore the expansion of the human climatic envelope. Humans learned how to build shelters, where they could retreat and store food and animal grease for fire, and thus they became the main predator. At the end of PHT humans had already learnt how to hunt all species and how to survive in any environment. The most striking example of this is an early Holocene archeological site on the small island of Johovo, 500 km north of the

Arctic coast (76°N, 153°E). Armed with bone tools, these people lived in those extreme conditions, mostly hunting polar bears (Pitul'ko 1993), which are three times larger than the cave lion, and 10 times larger than the hunters themselves. If humans could regularly (i.e., with little risk) hunt the biggest and most dangerous predators, in the most severe environments, it means they could hunt mammoths everywhere.

Human expansion north in geographical space reflected climatic changes. People were likely absent or rare in the homogeneous northern Siberian plains in the cold epochs before the BWE. During the BWE the climate in northern Siberia and Alaska became similar to the glacial climate of Eastern Europe, and these territories became more suitable for human occupation.

The BWE also sharply changed the landscape. Permafrost degradation led to numerous badlands (see Fig. 10.2), thermokarst lakes with steep cliffs (Fig. 10.1) and canyons. These changes would not have affected most animals; however they provide huge advantages for hunters. Heterogeneous landscapes provide better opportunities for hunters to closely stalk their prey. The landscape also became better for cliff hunting. Falling from a cliff of only a few meters is sufficient for big herbivores to break their legs. Permafrost degradation would have created such cliffs every kilometer, such that chances for successful hunting were substantially increased. In the south for a long time humans were in equilibrium with other animals, but during extensive migration to the north and to America, experienced hunters met numerous animals that were likely unafraid of people and were potentially easier to kill.

Human expansion to the northern mammoth steppe occurred under conditions of unlimited resources. In such cases prey are often consumed irrationally. For example, bears that encounter abundant salmon, even being sated continue to hunt but eat only fattest part of the salmon head (pers. obs.). Our experiments on the Kolyma region have shown that if voles or ground squirrels have unlimited access to grains, they store them without limit. Evidence exists of reindeer extermination in northeastern Siberia in nineteenth century. When numerous reindeer herds were crossing big rivers, each hunter killed 70–100 animals daily. Only minor portions of the harvested meat were consumed, and reindeer carcasses that were killed only for skins were piled together into ramparts up to half kilometer long (Syroechkovskii 1986). At the same time in North America 50 million bison were exterminated. Why would one suggest that the ancestors of modern humans used prey more efficiently?

Animals in the mammoth steppe were very numerous, and if humans exterminated a substantial portion, then the north should preserve the evidence of that. However, calculating the probability of finding such evidence suggests otherwise. Assuming that on average over each square kilometer humans killed 1–2 mammoths and 10 bison. However on the same territory 1,000 mammoth and 20,000 bison skeletons that died over the course of the late Pleistocene through natural causes are also preserved. In a collection such as presented in Fig. 10.10, finding bones from animals killed by humans is unlikely.

The yedoma plains do not have lithic resources. Therefore, it is likely that for hunting (similarly to Zhokhov Island) bone tools were mostly used. Assuming that killing and dressing 10 animals required ~100 bone tools. Bone tools are "small bones" – similar in size to bison ribs; so the probability that they persisted in permafrost is low – one out of hundreds (Fig. 10.11) – leading to the persistence, on average, of no more than several bone artefacts per square kilometre. Even specialists can overlook these artefacts among mudflows and millions of other bones. To find one such artefact it would be necessary to gather tens or even hundreds of collections such as ours (Fig. 10.10). Also it should be mentioned that in contrast to Alaska, in northern Siberia, in the BWE accumulation of loess stopped (Sher et al. 2005) and any evidence of human activity remaining on the surface would have decayed.

Predators in the mammoth steppe used all of the herbivores (including soft bones) and therefore they could exist in high densities; however only few of their bones are preserved in permafrost. In all of the collections gathered from the Siberian north, there were only several tens of bones from wolves and lions. Human bones are similar in size to those of wolves and lions, but periods of active animal extinctions were 100 times shorter than the time of yedoma accumulation. Therefore even at rational resource consumption rates by humans the probability of finding a mammoth hunter bone is hundreds of times smaller than the probability of finding wolves' or lion's bones, and human bones should be absent in these collections.

If we assume that the bigger part of mammoths in PHT died during cliff hunts, and under every cliff suitable for hunting 50 mammoths died (in the Berelyokh mammoth graveyard are the remains of over 160 mammoths, on Achchaghyi-Allaikha graveyard over 28 mammoths (Nikolskiy et al. 2009)) then on the Siberian plains there should be on average one such cemetery for every 50 km^2, and roughly the same density of archaeological sites should be found. What is the probability of encountering such sites? Annually, 20–30 t of tusks are collected on the yedoma plains (Boeskorov et al. 2008), and the density of tusks in the yedoma is 10 t/km^2, indicating that on average 2–3 km^2 of eroded yedoma would be surveyed annually. From this we calculate that the probability of encountering a mammoth graveyard is very small, only one graveyard discovery every 17–25 years. Since 1947 scientists have discovered three mammoth graveyards (Nikolskiy et al. 2009), in line with such estimates.

The highest density of ^{14}C mammoth dates in the Siberian north is recorded for the BWE (after 12,600 ^{14}C years BP) (Figs. 10.5, 10.12). But it is interesting to note that all of the dates that were found to the south of 73°N are found either in mammoth cemeteries or in archeological sites (Kuzmin et al. 2001; Sher et al. 2005; Nikolskiy et al. 2009). This data indicates that to the south of 73°N mammoths died because of humans and became extinct during the BWE, while to the north of 73°N (western Siberia, Taimyr and northern islands) mammoths died of natural causes and persisted (Kuzmin et al. 2001; Sher et al. 2005). And humans arrived there only after the sharp climate warming subsequent to the end of the Younger Dryas cold period. All our estimates are very rough, but they indicate that in northern Siberia there were enough people to cause a decline in the herbivore population, thereby decreasing pastures and ecosystem productivity, with the eventual extinction of mammoths and bison.

The modern climate of north-eastern Siberia, central Alaska and Yukon Territory is likely the climatic optimum for the mammoth steppe (Fig. 10.6). In colder and dryer conditions pasture productivity declines, while in warmer and wetter conditions, it would be harder for animals to excavate deep snow while grazing for forage, and it would be harder to prevent trees and shrub expansion. Holocene climate warming became fatal for the mammoth ecosystem, because with warming humans penetrated the north.

10.13 The Future of the Mammoth Steppe

It was in the rich pasture ecosystems that modern humans first appeared, and civilizations were born in this ecosystem. The mammoth ecosystem was one of the first victims of the exploitation of grasslands. Humans reduced animal numbers, and mossy forests and tundra replaced grasses. Different megafauna species became extinct with arrival of humans or new technology on different continents (Barnosky et al. 2004). In many places animal biomass decreased and pastures ecosystems turned to woodlands. We suggest that because grasses were no longer grazed they began to reproduce via seeds more aggressively. By exterminating animals humans may have lost a source of meat, but a new feeding niche opened up. The appearance of agriculture and the domestication of animals and the artificial control of biocycling negatively impacted pasture ecosystems. From an ecological point of view these agricultural ecosystems are simple: they have few species, and biological competition is suppressed. However one could consider that there is direct competition between agricultural ecosystems and their wild counterparts for territory and fertile soils. Today almost all meadows, steppes and prairies are tilled or converted into domestic pastures and hayfields. In Africa grassland ecosystems have been moved to nature reserves. Near civilization only those animal species that can hide in forests, mountains or in dry deserts have survived.

It is frequently stated that in the past people lived in harmony with nature. For example, when native Siberian hunters, Yukagirs, drove reindeers to the lakes, they always let one reindeer go (Syroechkovskii 1986). But only one and the rest were killed. Reindeers persisted there only because Yukagir weapons were primitive. It wasn’t a harmony it was equilibrium. The majority of people have forgotten about grassland ecosystems and their associated animals outside of Africa. For most, wild nature is a forest with songbirds or desert with lizards, and tundra is considered an untouched habitat. However in Russia, for example, the majority of tundras are pastures for domestic reindeers. Wild reindeer are the primary pest of domestic herds and regardless of prohibitions are actively killed by reindeer herders. Besides lemmings and hares, of the wild herbivores found in the Russian tundra only geese have persisted, but even they are losing places for wintering and have been substantially reduced in number. Lemmings and hares cannot maintain active biocycling on the tundra; therefore lichens and mosses now dominate these ecosystems.

Only 100 years ago, hunters were killing hundreds of animals in Africa for sport and in Europe were treated like Olympic champions. The famous explorer Prjevalskii was one of the last to see the wild pasture ecosystems (see epigraph). But he not only discovered new animal species, he also exterminated them. Based on his reports he shot every single animal or bird he met during his journeys. “Usually, I placed on the boat nose and continuously sent greeting all creation I have met on my way either from fowling piece, or from carbine depending on distance.” (Przhevalsky 1947, p. 10). A few hundred such explorers could exterminate all animals in any pasture ecosystem. Now everyone is ready to preserve nature; however there is almost nothing left of the wild. Most commonly it is some form of plant assemblage, with no or very few big animals or birds in it, who have a minimal impact on the environment. Therefore to preserve nature one should first recover biological diversity.

Atmospheric content and the planet’s climate is changing, and pollution to ecosystems increases. The population of the planet has just reached seven billion people. Many existing ecosystems can’t be preserved in their current locations, as they would change. It is easiest to preserve that which is of no interest to anyone, like polar deserts. But it is most important to preserve the most precious. The basis of our civilization is grasses and herbivores. The majority of domestic plants and animals, as well as humans, originated from pasture ecosystems. This is the motherland of civilization. These ecosystems should be under the biggest protection. But how do we protect something that doesn’t exist anymore? Today many of the species that are considered native to pasture ecosystems exist only in zoos and on farms. In these places we can preserve what the animals looked like in the wild, but not how the animals migrated, how they defended themselves from predators, how they competed with others, how they resisted parasites and various toxins. Animals should be preserved in ecosystems. But first these ecosystems must be recovered.

Can complex, self-regulating grassland ecosystems be recovered in the mid-latitudes? Technically yes. In a region with a suitable climate reserves should be delineated, and as many species which had previously lived in similar conditions should be assembled there. These animals would then fill the niches in the reserve according to their functional groups. In such a scenario, all the animals need not be from one regional community. Currently, many of the species in wild ecosystems are immigrants from other regions: e.g., horses moved to Siberia from America. Nor need it be purebred species. They could be of various breeds, feral or domestic animals. For example wild horses became extinct in America 12,000 years ago, but mustangs subsequently successfully occupied their niche. Right now we are not capable of constructing new ecosystems. But components of pasture ecosystems are capable of self-construction and evolution.

The question is only where to do that. Pasture ecosystems can be sustainable only on very big territories. Good agricultural land is very expensive. In Europe one probably place where pasture ecosystems can be revived is the region around

Chernobyl'. In the United States on the west of Great Plains agriculture is experiencing serious problems and the possibility of reconstructing pasture ecosystems there is being seriously discussed (Donlan et al. 2006).

Wild nature should be preserved from poachers. On the other hand, truly wild ecosystems could threaten nearby agricultural and pastoral land. For example, it is enough for one diseased bison to escape and an entire region would be closed for quarantine. Reliable fences are needed for the harmonious co-existence of civilization and wild nature.

The vast plains of northern Siberia, Alaska and Yukon are reliably fenced from agricultural land and pastures with snowy ridges. The climate of these territories is close to the optimum for northern pasture ecosystems, and they can be revived there. Modern soils there are poor in nutrients, but the underlying mammoth soils are an order richer in nutrition. As soon as mammoth soils thaw they are overgrown by grasses. Grasses prevent erosion, but they cannot prevent permafrost degradation. However if other grasslands exist somewhere nearby with abundant herbivores, then herbivores will migrate to the thawing permafrost. In the winter they would excavate snow looking for forage, and would strongly compress it, promoting permafrost cooling. Already there is enough forage for millions of bison, horses, musk-ox, elk, reindeers, moose and snow goats. All that is needed is to gather and settle them in their former areas and to maintain their conservation, and with time animals would fill all existing ecological niches. Animals would increase grassland productivity, and finally would densely fill these grasslands, as back in the Pleistocene.

The rebirth of pasture ecosystem is probably the only way to preserve the permafrost. Moreover, during the peak of the last glaciations, pasture ecosystems dominated the planet, and the biggest of these was the mammoth steppe ecosystem. Atmospheric concentration of CO_2 and CH_4 was substantially lower than in Holocene (Solomon et al. 2007). Albescent pasture ecosystems promote the planet's cooling. They can be very useful to combat current climate warming. They can absorb more carbon from the atmosphere than forests and can reliably preserve this carbon from fires in the deep soil. These ecosystems must be returned to nature.

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