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Article

Ecological Constraints and Drivers for Human Dispersals and Adaptations in the Late Pleistocene and Early Holocene Environments of the East Siberian Arctic

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Abstract: Starting roughly 50,000 years ago, the Arctic region of East Siberia remained continuously populated by groups of anatomically modern humans including the most uncomfortable episodes in the development of the late Quaternary environment; for some of them, human presence in the area became ephemeral. At present, archaeological fossil records allow for distinguishing three main stages in human occupation of the area: Early (~50 to ~29 ka, MIS 3), middle (~29 to ~11.7 ka, MIS 2), and late (from 11.7 to ~8 ka). For most of the time, they the populated open landscapes of the Mammoth Steppe, which declined at the onset of the Holocene. Human settlement of the Arctic was driven by various abiotic and biotic factors and thus archaeologically visible cardinal cultural and technological changes correspond to the most important paleoclimatic and habitat changes in the late Pleistocene and early Holocene. Successful peopling of the Arctic was largely facilitated by the adoption of critically important innovations such as sewing technology based on the use of the eyed bone needle and the manufacture of long shafts and pointed implements made of mammoth tusks. Mammoth exploitation is seen in mass accumulations of mammoths formed by hunting. An obvious connection between archaeological materials and such accumulations is observed in the archaeological record. In the lithic technology, the early stage is presented by archaic-looking flake industries. Starting the LGM, the wedge-core based-microblade technology known as the Beringian microblade tradition spread widely following the shrinkage of the mammoth range. At the late stage, starting at the Holocene boundary, microprismatic blade technology occurs. In all stages, the complex social behavior of the ancient Arctic settlers is revealed. The long-distance transport of products, knowledge, and genes occurs due to the introduction of the land transportation system. Initial human settlement of this region is associated with carriers of the West Eurasian genome who became replaced by the population with East Asian ancestry constantly moving North under the pressure of climate change.

Keywords: arctic Siberia; late Pleistocene; early Holocene; Stone Age; Upper Palaeolithic; human dispersal; adaptations; mammoth; critical technology; complex human behavior

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1. Introduction

The Arctic territory is an area occupied by many variations of the tundra biome from the sparse Arctic, common on the coasts of the Arctic Ocean and some islands, to relatively richer variants of shrub tundra and forest tundra in the southern areas of the region [1]. Since the beginning of the scientific study of this area of the planet approximately 400 years ago, European and Russian travelers and researchers have learned that these territories, despite the severity of the climate and limited natural resources, were actually inhabited by humans throughout their entire length. At the same time, the assumption occurred that people had lived there for a long time—in a certain sense, always—and a natural desire developed to find out when people first came to the Arctic, and who these people were.

The volumes of archaeological evidence on the basis of which it is possible to judge the processes of human settlement in the Arctic as a whole (from the initial stage to historical modernity) are quite large, but they are unevenly distributed [2]. In addition, sometimes there is a significant chronological gap between the evidence of the initial human occupation of the area and the continuous archaeological chronicle documenting their permanent stay in certain regions of the Arctic. In some cases, such gaps span tens of thousands of years, which is typical, first, for the western edge of the East Siberian Arctic—the Taimyr Peninsula [3].

The chronicle of human settlement in the Arctic spans approximately 50,000 years [4–7]; hereafter, the calendar ages are used. Geographically, archaeological finds are associated with Arctic territories to the west of the Beringian Land Bridge, which once connected the Euro-Asian and North American continents—a paleo-geographical, zoogeographic, and floral phenomenon of the Late Pleistocene of the Holarctic [8–16]. These data characterize the final stage of the global process of settlement of anatomically modern humans. Thus, the Arctic regions of Northern Eurasia were settled, human migration to the New World took place [17,18], and finally, the Arctic territories of America and Greenland became inhabited. As a result, the Eastern Hemisphere was completely mastered by people; the Western Hemisphere was also discovered and populated [19,20], although the participants of that process did not suspect this. Thus, the Arctic territories turned out to be the scene of the most important events in the history of mankind. On the scale of geological time, this process covers a significant part of MIS 3 and MIS 2 (the second half of the late Pleistocene) and ends in geological modernity, in the Holocene (MIS 1) (Figure 1). At the same time, in the second half of the Holocene, the population was mainly redistributed in previously populated areas, often associated with the influx of new human groups moving in a northerly direction. The main goal of the article is to determine the most important events in the history of the human settlement of East Arctic Siberia based on the ages of known archaeological evidence and the geographic position of archaeological sites, discuss these in relation to the past environment and climate change, and reconstruct the population history of the study area.

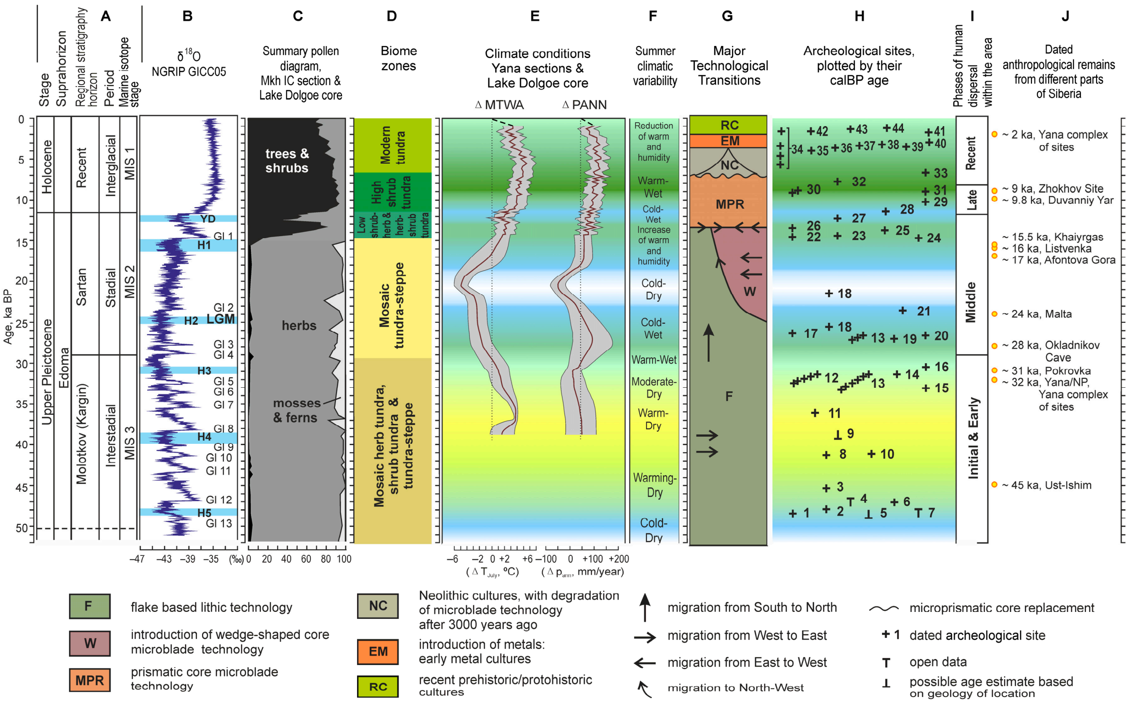

Figure 1. Climatic, paleoenvironmental, and archaeological record of the East Siberian Arctic. (**A**) Regional stratigraphic scheme of the Yano-Kolyma lowland and its mountain framing, after Stratigraphic

Code... [21]; (**B**) NorthGRIP δ18O scale and the sequence of Greenland interstadials (GI1–GI13), according to Svensson et al. [22], blue bands mark the approximate position of the Younger Dryas cooling (YD) and Heinrich events (H1–H5) according to Tierney et al. [23]; (**C**) general composition of palynospectra retrieved from Quaternary sediments of Mkh IC section, according to Sher et al. [24] and bottom sediment core from Dolgoe Lake, after Pisaric et al. [25], Klemm et al. [26]; (**D**–**G**), after Pavlova and Pitulko [16]: (**D**) biomes; (**E**) paleoclimatic reconstructions based on paleofloristic analysis: ΔMTWA—deviation of air temperatures of the warmest month (°C), ΔPANN—average annual precipitation (mm/year); (**F**) total climate change; (**G**) archaeological record of the East Siberian Arctic; (**H**) archaeological objects according their calendar age; (**I**) phases of human dispersal within the area; (**J**) dated anthropological remains from various regions of Siberia. For (**H**), dated archaeological sites are indicated: 1—Sopkarga mammoth, 2—the locality of Bunge-Toll-1885, 3—Kyuchus, 4—Upstream Point, Yana complex of sites (YCS), 5—Zyryanka, 6—Irelyakh-Siene, 7—Bolshoy Anyui, 8—New Siberia/West, 9—New Siberia/East, 10—AL044-2005 site, 11—Omoloy, 12—Yana complex of sites (YCS): Northern Point, Yana B area and Yana mammoth "graveyard"/YMAM, 13—Diring-Ayan, 14—Buor-Khaya/Ortho-Stan, 15—Kastykhtakh mammoth, 16—Tabayuryakh mammoth, 17—Lagernyi Point/YCS, 18—Yana A area/YCS, 19—Ilin-Syalakh 034, 20—Wrangel island, 21—Zyryanka 1, 22—Urez-22, 23—Ilin-Syalakh, 24—Achchaghyi-Allaikha, 25—Berelekh geoarchaeological complex; 26—Nikita Lake, 27—Cape Kamennyi, 28—Tytylvaam IV, 29—Naivan, 30—Zhokhov site, 31—Chelkun IV, 32—Tuguttakh, 33—Tagenar VI, 34—Siktyakh I, 35—Rodinka burial, 36—Chertov Ovrag, 37—Burulgino, 38—Rauchuagytgyn I, 39—Pegtymel, 40—Aachim-base, 41—Aachim-lighthouse, 42—Cape Baranov, 43—Pegtymel cave, 44—Shalaurova Izba, after Pavlova and Pitulko ([16]: Table 1) (with modifications based on Pitulko et al., 2015 [27]), Pitulko and Pavlova 2016 [28], Novgorodov et al. [29], Cheprasov et al. [30,31], Pavlov and Suzuki 2020 [32], Chlachula et al. [33], Kirillova at al. [34]; Pitulko et al. [35,36], Dikov [37], Кирьяк [38], Khlobystin [39], Gusev [40]. Geographic locations of the sites are indicated on the maps organized by time slices.

2. The Early Stage of Human Settlement in the East Siberian Arctic (~50–29 ka)

The specified interval (termed Molotkovskii (Karginskii) interstadial in Russian chronostratigraphic scheme of NE Siberia) was warmer and wetter than the beginning of MIS 3 in terms of temperature and humidity; in Arctic West Beringia, an ecosystem of open spaces was formed, dominated by herbaceous vegetation, [41], which was favorable for the existence of megafauna. Throughout its entire stretch from the northern to the inner southern regions at that time, against the background of an arid climate, dry grass-sedge tundra-steppe prevailed under developing warming conditions (Figure 1A–F), where woolly mammoth (*Mammuthus primigenius* Blumenbach), Pleistocene bison (*Bison priscus* Bojanus), and Pleistocene horse (*Equus caballus* L.) lived [24,42–46].

For local mammoth and bison populations, based on the frequency of dating, a close increasing trend of changes in relative abundance was established, quickly reaching maximum values [47]. At this time, the relative abundance of the mammoth population was rapidly increasing, and approximately 45,000 years ago reached a historical maximum in its history of existence [48]. A biome of the mammoth steppe formed, which played an important role in human settlement in Northern Eurasia. Its development was determined by the alternation of relatively warmer and relatively colder periods, during which the features of similarity in vegetation and landscapes were preserved throughout the territory it occupied, but with simultaneous diversity of local conditions [49].

The early phase of the MIS 3 interstadial (57–45.7 ka) includes the archaeological materials listed here from west to east, obtained from the following locations: Sopochnaya Karga (~48.3 ka), Bunge-Toll-1885 (~48 ka), Kyuchus (~45.2 ka), the Upstream Point of the Yana complex of sites (>46.6 ka), Zyryanka (~49 ka), Irelyakh-Siene (~47 ka), and Bolshoy Anyui (~48.4 ka) (Figure 1H—1–7, accordingly). The most reliable among them are Sopochnaya Karga and Bunge-Toll'-1885 locations, the Upstream Point of the Yana complex of sites, and finds from Zyryanka and Irelyakh-Siene sites. An age estimate for the first three sites is supported by direct dates on the artefacts or bone remains associated with human activity, while the geological age of the archaeological materials from Zyryanka and Irelyakh-Siene is controlled by the stratigraphic context of the locations. All of them indicate for this interval the presence of man in the area from the present mouth of the Yenisei River to Western Chukotka (Figure 2A). This evidence was dispersed over ~3000 km and appeared approximately simultaneously, within one to three thousand years. The pace of human settlement in the territory, therefore, was very fast.

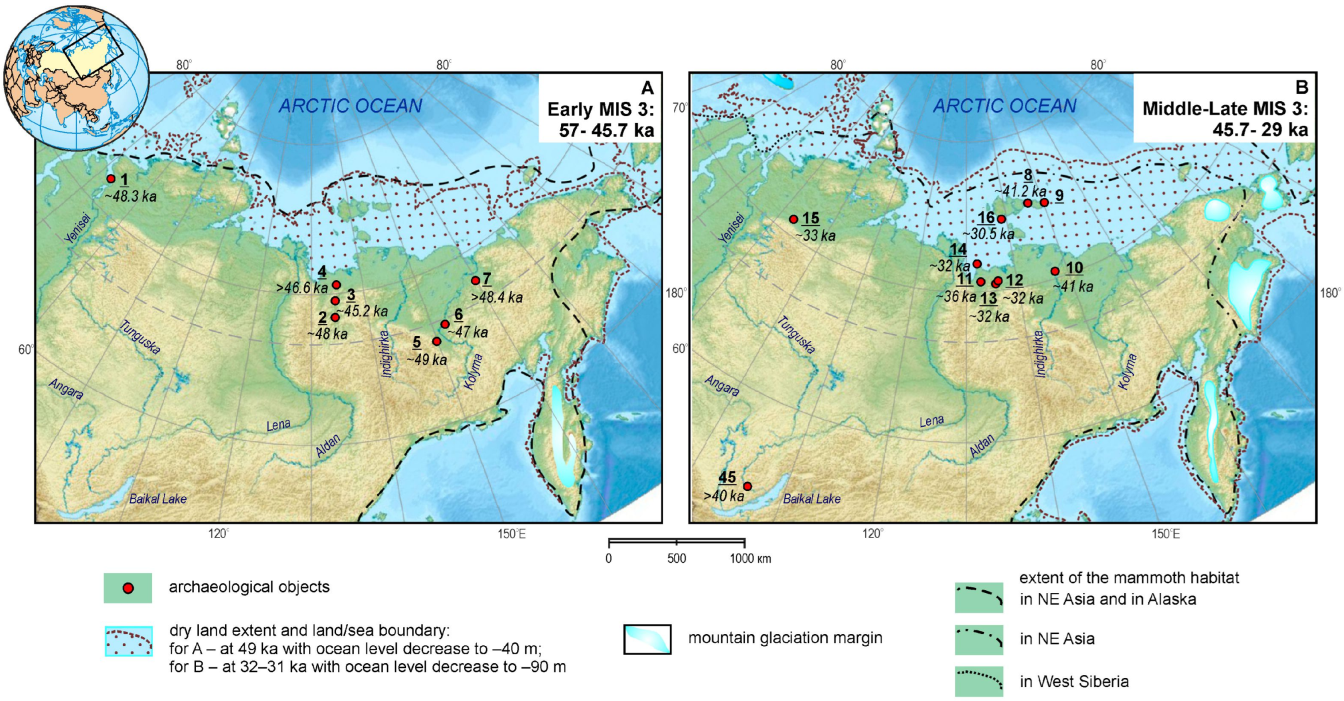

Figure 2. Early stage of the human settlement of the arctic East Siberia and MIS 3 paleoenvironments of the area. (**A**) Locations that yielded evidence of human presence during the early MIS 3 interstadial (57–45.7 ka). Paleoenvironments: dry land extent and land/sea boundary at 49 ka with ocean level decrease to −40 m is based on Pico et al. [50]; mountain glaciation margin, after Barr and Clark [51], Galanin [52]; extent of the mammoth habitat: in NE Asia and in Alaska, after McDonald et al. [53]. Dated archaeological sites are indicated: 1—Sopohnaya Karga mammoth, 2—the locality of Bunge-Toll-1885, 3—Kyuchus, 4—Upstream Point, Yana complex of sites (YCS), 5—Zyryanka, 6—Irelyakh-Siene, 7—Bolshoy Anyui. (**B**) Locations that yielded evidence of human presence during middle and late MIS 3 interstadial (45.7–29 ka). Paleoenvironments: dry land extent and land/sea boundary at 32—31 ka with ocean level decrease to −90 m is based on Pico et al. [50]; mountain glaciation margin, after Barr and Clark [51], Galanin [52]; extent of the mammoth habitat: in NE Asia and in Alaska, after McDonald et al. [53], in NE Asia, after Pitulko, Nikolskiy [54], in West Siberia, after Kahlke [55]. Dated archaeological sites are indicated: 8—New Siberia/West, 9—New Siberia/East, 10—AL044-2005 site, 11—Omoloy, 12—Yana complex of sites (YCS): Northern Point, Yana B area and Yana mammoth "graveyard"/YMAM, 13—Diring-Ayan, 14—Buor-Khaya/Ortho-Stan, 15—Kastykhtakh mammoth, 16—Tabauyriakh mammoth. Archaeological sites of that time in South Siberia: 45—Makarovo IV. Location of the sites and their age estimate is based on Pitulko et al., 2016b [3], Pitulko [4], Pavlova and Pitulko [16], Cheprasov et al., 2015 [30], Cheprasov et al., 2018 [31], Pavlov, Suzuki 2020 [32], Chlachula et al., 2021 [33], Kirillova et al., 2012 [34], Novgorodov et al., 2014 [29], Pitulko et al., 2015 [27], Pitulko et al., 2015 [56], Pitulko et al., 2017 [57], Goebel and Aksenov 1995 [58], Derevianko 1998 [59], Goebel et al., 2000 [60], Rybin and Khatsenovich [61]. Note numbers provided for archaeological sites are the same as shown in Figure 1H.

This is possible when occupying an ecological niche that was not occupied by anyone at the time of the arrival of the first settlers. Since there is no reliable evidence of the settlement of Neanderthals or other representatives of archaic forms of *Homo* in the Arctic, that is, no anthropological remains or archaeological finds north of 55° N exist [62–64], the assumption that there is a colossal free ecological niche in the Arctic region of the continent is at least acceptable. In such a situation, the rapid movement of population groups occurs in search of the best free land according to the scenario described for the historical Eskimo migrations [65], and it is possible only in a familiar landscape that does not require adaptation to an environment different from already known conditions.

As an example, it is necessary to cite Arctic Sea mammal hunters, who were very picky in the practice of using their ecological niche. The choice of a place for their settlement has always been conditioned by a number of necessary requirements (surface height, the scope of sea-level run-up fluctuations, the quality of the beach, freshwater, availability of basic resources, availability of alternative and/or complementary resources, availability of wood, etc.). Respectively, in the first place, locations were occupied whose physical characteristics corresponded to the list of requirements as much as possible. For this reason, such sites have existed for millennia; then as others, less convenient, began to be used forcibly, when the demographic capacity of the territory of long-term settlements was exhausted. In this regard, Krupnik [65] notes that the distance between settlements with long continuous habitation is, as a rule, very large.

This scenario may well be extrapolated on the model of settlement of the Early Upper Palaeolithic people, who began to explore the Arctic zone of Eastern Siberia at the beginning of the MIS 3 interstadial, with an almost simultaneous manifestation of the archaeological signal within the boundaries of the large region from Western Taimyr to Western Chukotka is connected (Figures 1H and 2A). The conditions for rapid human settlement were the relative uniformity of the landscape and faunal groupings living there, among which the most important for humans were large herbivores and the lack of competition for resources with other hominins. As a result, it turned out to be quickly dominated by people with an extremely low demographic density, which remained the norm throughout all subsequent periods and is true to the present-day Arctic.

Thus, approximately 2.3 million people currently live in the Arctic zone of Russia, with an average density of 0.63 people per square kilometer. Based on the historical records, for the territories of the whole of Siberia at the time of contact with the Russians, the local population is estimated at 250,000 people [66], and for the Siberian Arctic, this figure is an order of magnitude lower. It is impossible to reliably estimate the number of Arctic first settlers of the Upper Paleolithic; the only reference point in this regard is the result of a genome-wide study performed by Sikora and colleagues [67]. It is shown that the number of the entire human group, to which the residents of the Yana site belonged, did not exceed 500 people; at the same time, they knew how to circumvent the problem of inbreeding [67]. This knowledge was not unique since the same ability was established for the Upper Paleolithic inhabitants of the Russian Plain [68], i.e., its possession is one of the fundamental behavioral traits of anatomically modern humans.

The small amount of archaeological evidence, among which there are practically no settlement contexts, does not allow us to fully assess the features of the material culture of the population of the East Siberian Arctic at the initial stage of human settlement within its borders. Based on the findings from the Upstream Point of the Yana site and the location of Kyuchus [4,57], it can be said that, at that time, there were flake-based lithic industries of archaic appearance based on the splitting of pebbles, which were accompanied by bone-processing techniques and the technology of producing long shafts (rods, long points, and full-size spears) from mammoth tusks. Finds from sites at the early stage suggest that the basis of the life of these people was the hunting of various large herbivores—bison, horse, red deer (*Cervus elaphus* L.), reindeer (*Rangifer tarandus* L.), woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach), and woolly mammoth, but not the hunting of small animals such a hare (*Lepus tanaiticus* Gureev), i.e., in general, an economic model that fully corresponded to the one that existed subsequently for tens of thousands of years with changes corresponding to the fluctuation in the number of members of the faunal complex of the biome [69,70].

The most favorable natural climatic conditions of MIS 3 (MIS 3 optimum, that is, the interval covering 45.7–37.8 ka) are associated with the highest sea-level rise for the time of MIS 3 transgression [50]. The onset of the most favorable conditions and the duration of the MIS 3 optimum differed in time in different parts of the East Siberian Arctic, which was likely due to the degree of remoteness of these areas from the transgression front, the increase in the area occupied by the sea, and the effects of the deglaciation of the territories occupied by the Scandinavian/Barents Sea glacier [71,72].

During this period, sedge-grass and sedge-grass-forb tundra-steppe with a noticeable participation of shrubby willow were widespread [24,43–45,73,74]. The MIS 3 optimum in the northern part of the Arctic Western Beringia (Bolshoi Lyakhovskii Island) and its second half after 40.6 ka in the inner regions (within the present-day Bykovskii Peninsula and Yana-Indighirka lowland) were distinguished by the greatest number and diversity of mammoth fauna, represented by woolly mammoth, the Pleistocene horse, the Pleistocene bison, and reindeer [24,42–45]. In the range of 40–37 ka, a maximum number of woolly mammoths is noted everywhere [48,75].

Favorable conditions of the climatic optimum of MIS 3 apparently gave an additional impetus to the process of development of these territories by man. The population movement within the East Siberian Arctic at this time—new migrations into the area and possibly displacement of the population in already inhabited areas (Figure 2B)—can be judged by several facts, based on the dating obtained for the locations AL044–2005, Omoloi, New Siberia West, and New Siberia East (Figure 1H—10, 11, 8, 9, respectively), found in the space from the Yana site to the Indighirka River and on the New Siberian Islands [4,16,27,56,57]. Based on these few data, it can be concluded that the inhabited territory expanded to the north and embraced the area of the modern New Siberian Islands, for which there is correspondence in the above observations on the spatial dynamics of the habitats of the fauna contemporary with these people and the growth of the relative number of populations of the main hunted species.

In terms of the economic behavior of these people, it can be assumed that it has not undergone significant changes, but the data for this conclusion are minimal. The lithic industry is still flake-based, evident from finds at the Omoloi locality; rock-crystal is used (based on the finds from locality AL044-2005 in the Indighirka basin). In addition, on the island of New Siberia (localities West and East), cores from mammoth tusks were found 670 km northeast of the Yana complex of sites, from which long rods (points) were obtained, executed in classical Yana technology [56]. The age of one of these cores has been determined at ~41.2 ka.

The dominant process of transformation of the natural environment in the late phase of the interstage MIS 3 (37.8–29 ka) is the renewed decline in sea level. After 38 ka, it took on a growing exponential character, and at the end of MIS 3 by 29 ka, the decline reached marks 109–110 m relative to the modern sea level [50,76–78], in whose connection there was an increase in land area continued along the northern edges of the continent with a simultaneous increase in aridity in its interior (Figure 2B). Differences in the degree of moistening and, as a consequence, differences in the nature of vegetation cover, were determined by the position of individual territories in relation to the sea basin. During the late MIS 3 interstadial, sharply continental dry conditions existed in most of the territory, and in some time periods, wet conditions alternated with warm summer temperatures and severe winters with little snow [43,45,79]. This contributed to the widespread development of mosaic tundra landscapes at this time (Figure 1A–F). Plant associations were represented by forb-grass-sedge, wormwood-grass-sedge, and grass-wormwood-forbs communities, xeropetrophytic communities, local tundra communities in waterlogged areas, and sparse thickets of shrubby willow [16,80,81].

The rich herbage of the graminoid-dominated tundra steppe served as an excellent food base supporting the fauna of the mammoth complex, widespread throughout the territory of Western Beringia during the MIS 3 interstadial [24,42–44,48,57,71,82–85]. The most common species were the woolly mammoth, Pleistocene horse, reindeer, and Pleistocene bison. Woolly rhinoceros and musk ox were also encountered; among the predators were the wolf (*Canis lupus* L.), the polar fox (*Alopex lagopus* L.), the brown bear (*Ursus arctos* L.), the Pleistocene lion [*Panthera spelaea* (Goldfuss)], and a wolverine (*Gulo gulo* L.) [86,87]. During the late phase of MIS 3, there is a distinct dynamic change in the number and diversity of mammoth fauna in space and time [57]. In the inner regions of the Arctic of West Beringia (the Bykovskii Peninsula and Yana-Indighirka lowland), initially high numbers and diversity of mammoth fauna animals, represented by woolly mammoth, Pleistocene horse, bison, reindeer, gray wolf, and brown bear, were shrinking. After 31.3 ka, only woolly mammoth, Pleistocene horse, and reindeer remained in communities. The northern regions (the Bolshoy Lyakhovskii Island) are also characterized by a decrease in the diversity and abundance of mammoth fauna. Thus, if the woolly mammoth, Pleistocene bison, Pleistocene horse, musk ox (*Ovibos moschatus* Zimmerman), and woolly rhinoceros were represented between 37.8 and 33.2 ka, then only the woolly mammoth and Pleistocene horse were present by 29 ka [45,57]. The woolly mammoth population was characterized by the greatest constancy in spatial distribution and variations in abundance in the late MIS 3 thermochron, depending on climatic fluctuations [48,57,75].

Cultural remains of this time are represented in only two districts of the northwest Yana-Indighirka lowland. This is the Yana complex of sites [4,56,87–89] and the location of the Buor-Khaya/Orto-Stan on the west side of the Buor-Khaya Peninsula [35]; their age fits into the interval 33–31 ka (Figure 1H—12, 14, respectively; Figure 2B). The discovery of the Katystakh mammoth on the Taimyr belongs to the same time [34]; hunting lesions on its skeletal elements possibly indicate the presence of a human there on the eve of the last glacial maximum (Figure 1H—15).

The findings from the Buor-Khaya allow us to talk about the anthropogenic contribution to the formation of the bone-bed, which yielded modified mammoth bones, bones with traces of hunting impact, and skeletal elements with traces of butchering, as well as bison and horse bones. This is a rather expressive trace of human activity, replicating the behavior of the Yana site dwellers and indicating their widespread movement within the territory. The possibility of people moving great distances is documented by the finds of pendants made of exotic stone raw materials: Anthraxolite and amber. The nearest source of the first is located 300 km to the northwest in the area of the northeastern spurs of the Kharaulakh Range, and the source of amber is available only on the island of New Siberia, 670 km northeast of the Yana site [90]. The presence of people in the territory of modern New Siberian Islands on the eve of LGM is documented by the discovery of the Tabayuryakh mammoth (Figure 1H—16; Figure 2B) with a fragment of a throwing point embedded in its scapula [32]; in Taimyr, the most likely evidence of this kind is the injuries on the bones of the Katystakh mammoth [34].

The Yana complex of sites has a complicated spatial structure and contains several archaeological objects/localities, including seasonal residential zones—spring–summer, the Northern Point locality [91], and winter, the site of Yana "B" [88], as well as the mass accumulation of mammoth bone remains, YMAM. This object was formed as a result of human activity, as an area for storing and preliminary preparation for processing the results of mammoth hunting, that is, different body parts including complete heads with tusks [56,92,93].

The material cultural remains of the Yana complex, according to observations made at the Yana "mammoth graveyard" (YMAM) and during excavations at the Northern Point and Yana "B" sites, include four main technological contexts: (1) The production of multifunctional tools (scrapers) used for processing hunted prey and various materials, of which the most remarkable are backed forms [90,94]; (2) the production of micro tools for processing diverse osseous materials such as mammoth bones and tusks (ivory), and reindeer antler, as well as for creating elements of hunting equipment [89]; (3) the production of artifacts from mammoth tusk, bone, and antler [56,91,95]; and (4) the production of red "ochre" [90]. There are no visible dwelling structures; however, there are hearths and evidence related to them, or of a "fire use context".

The stone industry, based on the splitting of pebbles, has a pronounced flaking character and an archaic appearance—discoid, pyramidal, and orthogonal cores made of pebbles readily available on the beach next to the site area comprising a variety of local rocks. It is complemented by the limited use of rock crystal (available in the area approximately 50 km southward), mainly for processing tusks, as well as the production of ochre. The processing of the tusk and bone is represented by a massive series of functional (points, needles, and awls) and non-utilitarian objects (beads, pendants, 'diadems', bracelets, and figurative art), forming a phenomenal quality context of symbolic behavioral manifestations. On the basis of the materials from the Yana site, critical technologies that provided the possibility for the stable existence of these people in the conditions of the Late Pleistocene of the East Siberian Arctic have been reconstructed [56,91,96].

The basis of the economic activity of this population was hunting for Pleistocene bison, horses, reindeer, woolly rhinoceros, and woolly mammoth. Hares were caught in a variety of ways, but only as raw materials for sewing production; in the cultural sediments of the site, there are many skeletal deposits of hares from which the skin was removed [90]. In the cultural practice of the Arctic peoples, it is a valuable raw material for tailoring undergarments [97].

Mammoth hunting was carried out for its tusks, which were an important raw material resource as a substitute for wood [56], completely absent in the open landscapes of the mammoth steppe but extremely necessary for the creation of objects of the hunting equipment complex. In the series of dating mammoth bone remains from the YMAM, there are no indications of mass one-time hunting. In contrast, they indicate a gradual accumulation of bone remains in that special area of the Yana site complex [56,93]. Despite the fact that the mammoth was obviously eaten, it was not the main food resource. As such, bison, horses, and reindeer have appeared at different times [90–92].

3. The Middle Stage of Human Settlement in the East Siberian Arctic (~29–11.7 ka)

The MIS 2 spanning 29–11.7 ka (for East Siberia, it is also termed Sartan cryochron in Russian nomenclature) is characterized by the development of environmental conditions in the regime of progressive global climate cooling [98,99] against the background of ongoing deepening of the sea level, which by 24 ka had decreased to its minimum and reached a position of 129–130 m relative to the modern level [50,76–78]. In the inner part of the Arctic Western Beringia in the area of the Yana complex of sites, the MIS 2 stadial was characterized by the spread of mosaic landscapes of low-yielding grass-sedge tundra steppes (Figure 1A–F), where Arctic, aquatic, coastal, meadow, and steppe taxa were combined. In the conditions of a dry cold continental climate, there were widespread cryophytic grass-wormwood and wormwood-grass communities with the inclusion of forbs, dryad tundra, and xeropetrophytic and nival communities, which together had a tundra-steppe appearance [80,81,100]. The coldest and driest climatic conditions of the LGM in this area appeared after 24 ka and persisted until 18.2 ka.

During MIS 2, local climates of the East Siberian Arctic developed under conditions of increasing sharp continentality and at the initial stage of 29–24 ka was cold and wet. The average July temperatures were 1–4 °C lower than current temperatures and the annual precipitation exceeded the current values by 100–175 mm [28,100–103].

The time of the glacial maximum was characterized by a decrease in the number and diversity of mammoth fauna. However, woolly mammoths were widespread everywhere in the Western Arctic of Beringia; the presence of woolly rhinoceros and Pleistocene bison was noted in some periods in its interior. In the north, Pleistocene horses were often found, and occasionally woolly rhinoceros were found [43,45,57]. Based on the analysis of the mass results of radiocarbon dating of mammoth bone remains, changes in the relative number of populations of these animals and the dynamics of their areas of settlement have been reconstructed. Thus, an increase in the number of mammoths is noted at the beginning of MIS 2 in the extreme north of the Arctic Western Beringia (New Siberia Islands); the relative population size reaches peak values at the same time with the onset of extreme climatic conditions of the LGM. During the last glacial maximum, the number of mammoths decreased, and approximately 18.2 ka, they became invisible in the paleontological record. After the end of extremely harsh conditions, the number of mammoths began to recover [48]. In the inland continental areas (the Yana-Indighirka lowland), there was a progressive decrease in the number of mammoths from the beginning of the MIS 2 stadial to the end of the LGM cooling maximum around 18.2 ka [48,57].

The East Siberian Arctic includes a rather large number of locations and sites represented by two groups (Figure 3A,B). The first characterizes the presence of people at an early stage and specifically at the maximum of cooling; these are the Diring-Ayan, Yana "A" area, and Lagernyi localities in the Yana cluster of sites, Ilin-Syalakh 034 [27,57], the upper horizon of the location of Zyryanka-1 [33], and the discovery of a punctured scapula of a mammoth on Wrangel Island [84] (Figure 1H—13, 17, 18, 19, 21, 20, respectively; Figure 3A). They belong to the era of the harsher environmental conditions, the Last Glacial Maximum, and their age is in the range of 27–23 ka. The listed localities serve as evidence of the presence of people, but it is gradually decreasing; among these locations, there is not one whose materials would allow for judging the culture of these people in detail. Nevertheless, it is obvious that they steadily carried out hunts for the mammoth (the scapula from Wrangel Island and evidence from the Ilin-Syalakh 034 site); they had a technology of production of long points and full-size spears of mammoth tusk, which can be argued on the basis of the discovery of a fragment of the mammoth tusk core at the Lagernyi locality of the Yana site. Furthermore, at least in some cases, they used the technology for the production of small blades) known from the Diring-Ayan location near the Yana complex of sites; their prey, in addition to the mammoth, became any available animals, primarily reindeer [57].

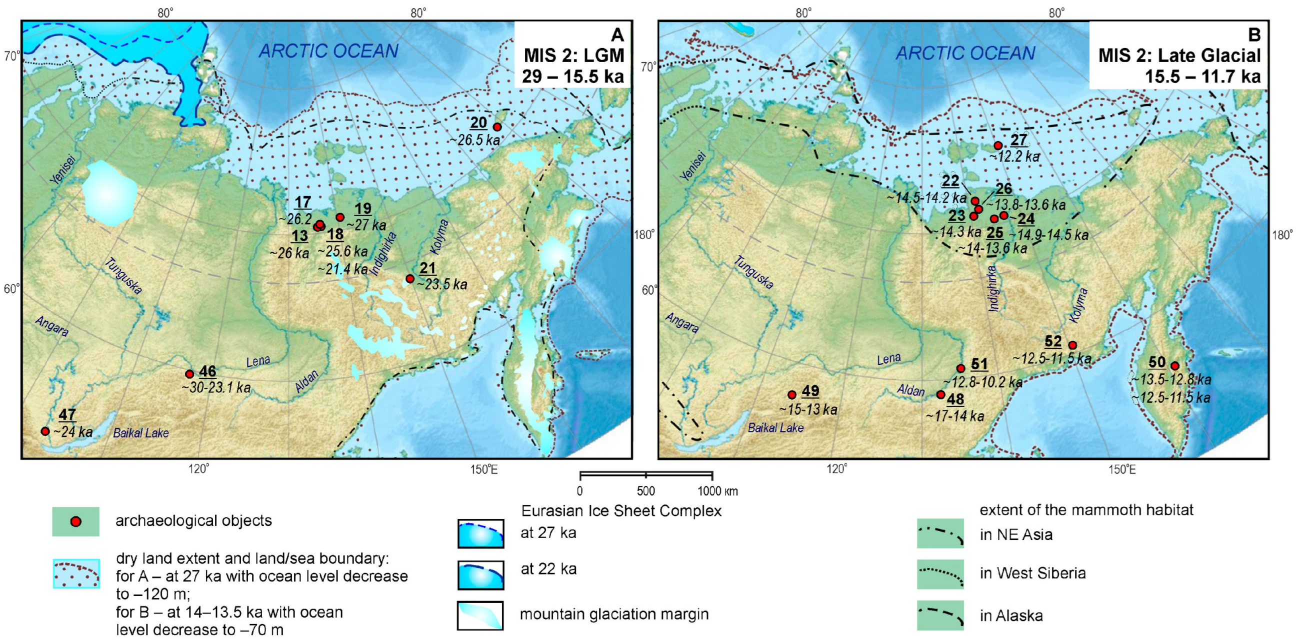

Figure 3. Middle stage of the human settlement in the arctic East Siberia and MIS 2 paleoenvironments. (**A**) Archaeological localities of the extreme cold phase of MIS 2 stadial (MIS 2 pessimum, 29–15.5 ka). Paleoenvironments: dry land extent and land/sea boundary at 27 ka with ocean level decrease to −120 m is based on Pico et al. [50]; Eurasian Ice Sheet Complex at 27 ka and 22 ka, after Hughes et al. [67] mountain glaciation margin, after Barr and Clark [51], Galanin [52], Glushkova [104]; extent of the mammoth habitat: in NE Asia, after Pitulko, Nikolskiy [54], in West Siberia, after Kahlke [55], in Alaska, after McDonald et al. [53]. Dated archaeological sites of the East Siberian Arctic are indicated: 13—Diring-Ayan, 17—Lagernyi Point/YCS, 18—Yana A area/YCS, 19—Ilin-Syalakh 034, 20—Wrangel island, 21—Zyryanka 1, after Pavlova and Pitulko [16], Cheprasov et al., 2018 [31]; Pitulko et al., 2016a [36]; Pitulko et al., 2015 [27]; Pitulko et al., 2017 [57]. Archaeological site of that time in South Siberia: 46—Khaiyrgas Cave, 47—Malta [102]. Site location

and age estimate provided based on Kuzmin et al., 2017 [105], Derevianko et al., 2003 [106], Raghavan et al., 2014 [107], Sitlivy et al., 1997 [108]. (**B**) Archaeological locations belonging to the late glacial stage of MIS 2 (15.5–11.7 ka). Paleoenvironments: dry land extent and land/sea boundary at 14–13.5 ka with ocean level decrease to −70 m is based on Pico et al. [50]; extent of the mammoth habitat: in NE Asia, after Pitulko, Nikolskiy [54], in West Siberia, after Kahlke [55], in Alaska, after McDonald et al. [53]. Dated archaeological sites are indicated: 22—Urez-22, 23—Ilin-Syalakh, 24—Achchaghyi-Allaikha, 25—Berelekh geoarchaeological complex; 26—Nikita Lake, 27—Cape Kamennyi, after Pavlova and Pitulko [16], Pitulko et al., 2016a [36], Pitulko et al., 2017 [57]. Archaeological sites in South Siberia confined to the same time span: 48—Dyuktai Cave, 49—Bolshoy Iakor, 50—Ushki site; 51—Ezhantsy; 52—Kheta. Site location and age estimate for them is based on Mochanov 1977 [109]; Ineshin and Tetenkin 2017 [110], Dikov 1979 [111], Slobodin 1999 [112] Note geographic pattern in which northern group of sites with a single microblade site (Urez-22) are located within the range of the local population of woolly mammoths, while in the archaeological contexts of the southern group outside the range of mammoths, narrow-front wedge-shaped core technology is confidently presented.

It should be emphasized that there is a chronological gap of approximately 10,000 years between the first and second groups of archaeological sites belonging to the MIS 2 (Figures 1H,I and 3A,B). However, there is no need to return to the discussion about the possible human depopulation of the region—the presence of people in it becomes ephemeral; thus, most of the evidence relates to the beginning of the extreme cold time slice of MIS 2 and there are only two in its middle. One of them comes from the Yana "A" locality of the Yana complex of sites, where the evidence for human presence dates to 25.6 and 21.4 ka [57] (Figure 1H—14; Figure 3A). Another one, documented by direct dating of a core made of a mammoth tusk, was found at Zyryanka 1 (Figure 1H—21; Figure 3A); it is ~23,500 years old [31]. In fact, this is a complete analogy to the gap observed in the paleontological chronicle of the local population of woolly mammoths, which, approximately 18,200 years ago, fell out of the biome but reappeared after the end of the period of extremely harsh conditions, but clearly, they were in the area all the time [48].

The late MIS 2 (15.5–11.7 ka) in Arctic Western Beringia is characterized by dynamic changes in the natural environment in accordance with the general global climate warming trend [98,99]. This is in relation to the progress and rate of deglaciation of the glacial cover of the Northern Hemisphere [71,113–116], the dynamics and amplitude of the rise of the sea level in general [50,78], and the development of the transgression of the Arctic Ocean [77,117–122].

The beginning of a fundamental restructuring of the natural environment in Western Beringia corresponds to the warming of the Bølling-Allerød Interstadial in Europe during the interval of 14.8–12.8 ka. In the Late Glacial period, tundra-steppe communities still retained their positions. However, the areas of moist meadow-shrub tundra with dwarf birch, tundra, and waterlogged meadows expanded [81]. Late glacial warming in the range of 13.7–12.8 ka, corresponding to the Allerød in Europe, was quite clearly manifested in the West Beringian Arctic.

The vegetation cover of the warm period of 13.7–12.8 ka was distinguished by a variety of tundra associations. In the north of the Western Beringian Arctic, dwarf shrubs sedge-grass tundra communities were developed with the inclusion of dwarf birch and shrub willow on the Bunge Land [16,123]; on Bolshoy Lyakhovskii Island, there were widespread grass-sedge and sedge-grass communities with the participation of shrubby willow and dwarf birch [41,45]. Vegetation in the western part of the Western Beringian Arctic was represented by birch shrub tundra in the lower reaches of the Lena River [25,26]; grass-sedge communities with the addition of wormwood, and shrub species of birch and willow in the area of the Oiyagos Yar [124]. Summer temperatures were above current temperatures by ~1–4 °C, and precipitation was 50–100 mm/year more than now [26,101].

Against this natural and climatic background was a second group of archaeological sites of the East Siberian Arctic, belonging to the final stage of MIS 2 (Figures 1A–I and 3B). It is composed of geoarchaeological objects of the northwest and north of the Yana-Indighirka lowland, whose geological age is in the range of 16.6–12.8 ka, while the episodes of human presence are chronologically even more compact and fit into the interval of 14.8–12.8 ka. These are the localities of Achchaghyi-Allaikha [125], Berelekh complex of geoarchaeological objects [126], locations of Nikita Lake, Urez-22, and Ilin-Syalakh [36,57] (Figure 1H—24, 25, 26, 22, 23 respectively). At the turn of the Holocene, the presence of people was noted in the New Siberian Islands, on the island of New Siberia, at Cape Kamenny locality, ~12.2 ka [16] (Figure 1H—27; Figure 3B). In the same direction, the southern border of the area of the local mammoth population shifted, and on the island of New Siberia, the presence of the last mammoths is noted, which finally fell out of the biome approximately 10,000 years ago [75].

A characteristic feature of the archaeological sites of the Late Glacial period in Arctic Eastern Siberia is their association with mass concentrations of mammoth bone remains (Figure 3B). For each of them, with the exception of Berelekh, a conclusion is made about their anthropogenic origin [36,92,125] as a result of human exploitation of local populations of these animals, i.e., hunting, which, as before that, was carried out for the sake of their tusks, which were used as raw materials for the production of long points. This conclusion is supported by various signs, including the undoubted sorting of bones [125], evidence of the production of long points from mammoth tusks, and direct evidence of hunting these animals [36].

The increase in the number of objects indirectly indicates that the human population has grown. Thus, people have become more active in this hunting, in which there are no signs of food exploitation of woolly mammoths. At the same time, each of the items contains the remains of clearly food species, sometimes in noticeable quantities: These are mainly reindeer and horses. At Berelekh, a huge quantity of bone remains is represented by hare, which, as at the Yana site, was most likely taken for the sake of the pelt for sewing raw materials. The material culture of this stage remains largely unknown. However, it can be noted that the technology of production of long rods from tusk is still relevant. In addition, for this time at the location of Urez-22, the presence of a developed form of the microblade industry [36] was noted for the first time in the East Siberian Arctic, likely in the form of lithic technology based on the wedge-shaped core idea. Interestingly, this is one of the earliest sites in the group; its age is ~14,500–14,200 years.

Sites in this group are characterized by the presence of specific small points, whose closest analogies are found outside the East Siberian Arctic (Western Beringia). Such examples are found in the American Northwest (eastern Beringif) at the sites of the Nenana complex (13.5–13 ka). They are quite numerous (for example, Dry Creek, Owl Ridge, Moose Creek, and Walker Road), and their number likely includes the sites of Broken Mammoth, Little John, and some others. The main feature of the stone industry in sites of the Nenana complex is the absence or small number of microblades and burins and the presence of teardrop-shaped and triangular points made of flakes, that is, incomplete bifaces known as Chindadn points [127–133].

In Western Beringia, they are represented at the sites of Berelekh, Nikita Lake, and Achchagyi-Allaikha. Thus, the time of existence of these well-recognized varieties is only approximately 1000 years, despite the fact that they are found from the Yana-Indighirka interfluve in Eurasia to the rivers of the Yukon basin in the northwest American continent. Interestingly, such expressive, short-lived cultural phenomena are not exclusive, so no less expressive Clovis sites have an even shorter history, in the interval of only ~13–12.7 ka, but very wide spatial distribution across mid-latitude North America [134,135]. Apparently, in both cases, the appearance of diagnostic artifacts is associated with changes in adaptations rather than with the appearance of new population groups. Regarding East Siberian sites with Chindadn points, it can be said that in Western Beringia, they appear in its Arctic region on the eve of the disappearance of the local mammoth population [36,93].

4. Late Stage of Human Settlement in the East Siberian Arctic (~11.7–8 ka)

In the Holocene, the development of the natural environment of Arctic Western Beringia occurred dynamically under the active influence of the oceanic post-glacial transgression, whose course and speed largely determined the appearance of the landscapes and the climate of this territory. At the beginning of the Holocene, approximately 11.7 ka, the sea level reached 52–53 m relative to the modern one [50]. Flooding and disintegration of the Arctic margin of Western Beringia have significantly accelerated [136].

A distinctive feature of the natural and climatic changes in the Holocene of the West Beringian Arctic is the early onset of the optimum in the interval of 11.5–10.2 ka on the New Siberian islands, first identified for Bolshoy Lyakhovskii Island [137] and Kotelny Island [138,139]. At this time, due to the significant warming and moisterization of the climate (Figure 1A–F), there was a significant movement of large shrubs (alder) and even tree-like birch to the north up to 75–76° N. July temperatures were 5 to 6 °C higher than at present, and landscapes were represented by subarctic grass-sedge-cereal-moss tundra and shrub tundra, where shrubby willow, birch (*Betula exilis*), and alder grew.

After 12.5 ka on the Yana-Indighirka lowland and the New Siberian Islands, according to all data available, tundra vegetation elements, represented by heather, appear in the landscapes, and the contribution of shrubby birch, willow, and alder sharply increases. Actually, this time was the boundary, after which the increase in temperature and humidity led to the final formation of tundra landscapes, the intensive development of thermoerosion, the discharge of thermokarst lakes, the formation of thaw-lakes in the territory, and the activation of peat accumulation [140–142]. The development of these processes led to the degradation of forage lands and provoked a reduction in populations of large herbivores in the biomes of the mammoth steppe—important for humans—and caused a shift in their habitats to the north [54,93].

Further changes in the landscapes of Northeast Siberia at the turn and at the beginning of the Holocene (Figures 1A–D and 4) were marked by the northward movement of the forest boundary, which, for a straight-stemmed birch, is approximately the same as the current position of the coastline [53,143]. In some areas, forest vegetation moved northward, occupying some modern Arctic islands [144].

At this time, the existence of populations of many species of Pleistocene herbivore fauna ended, which had served as a resource base for the population of the East Siberian Arctic for tens of thousands of years [53,69,70,75]. Actually, very soon, the reindeer turned out to be the most accessible species. In the dynamics of the ranges of large herbivore species, which subsequently fell out of the mammoth steppe biome [69], and the degradation of the biome itself [70], the northern trend became clearly visible. Thus, the last ‘patches’ of the mammoth steppe existed in the north of the New Siberian islands still approximately 12,000 years old. Simultaneously, the existence of the local population of woolly mammoths ended [16,75].

These events certainly caused stress for the population of the East Siberian Arctic. Human groups likely moved in the same direction, staying in the zone of well-known landscapes of open spaces, where animals familiar to them were still preserved. From the south, both those and others were squeezed out by woody vegetation, whose northern boundary of distribution at ~10.2 ka reached the position of the modern coastline.

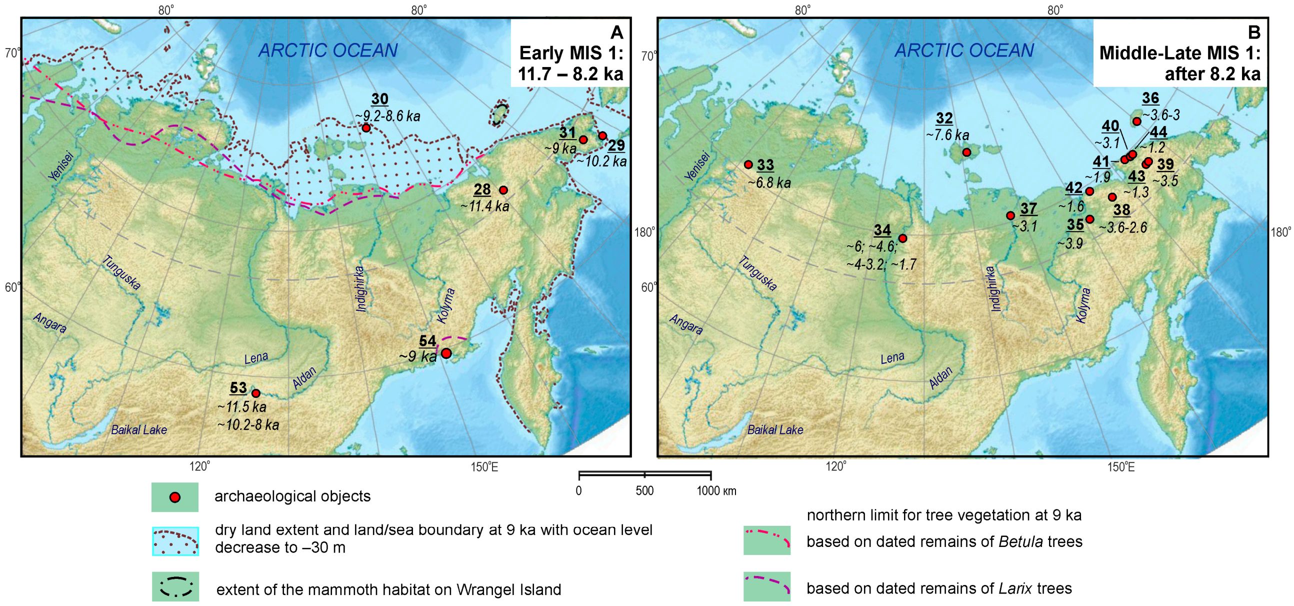

Figure 4. Late stage of the human settlement in the arctic East Siberia and paleoenvironments of MIS 1: (**A**) The Early Holocene archaeological sites (11.7–8.2 ka). Paleoenvironments: dry land extent and land/sea boundary at 9 ka with ocean level decrease to −30 m is based on Pico et al. [50], Bauch et al. [119]; extent of the mammoth habitat on Wrangel Island, after Vartanyan et al. [145]; northern limit for tree vegetation based on dated remains of Betula trees and Larix trees at 9 ka, after Kremenetski, et al. [146], Binney, et al. [147,148]. Dated archaeological sites of the East Siberian Arctic are indicated: 28—Tytylvaam IV, 29—Naivan, 30—Zhokhov site, 31—Chelkun IV, after Pavlova and Pitulko [16], Kiryak et al., 2003 [38], Dikov 1993 [37], Gusev 2002 [40], Pitulko 1999 [149]; Pitulko, Pavlova 2016 [28]. Archaeological site of that time in South Siberia: 53—Ust-Timpton; 54—Uptar I. Site location and their age estimate are provided based on Mochanov 1977 [109], Slobodin 1999 [112]. Objects are shown to estimate the time of the occurrence of microprismatic blade technology in the region. (**B**) Archaeological objects of Middle-Late MIS 1 (after 8.2 ka), dated archaeological sites are indicated: 32—Tuguttakh, 33—Tagenar VI, 34—Siktyakh I, 35—Rodinka burial, 36—Chertov Ovrag, 37—Burulgino, 38—Rauchuagytgyn I, 39—Pegtymel, 40—Aachim-base, 41—Aachim-lighthouse, 42—Cape Baranov, 43—Pegtymel cave, 44—Shalaurova Izba, after Pitulko and Pavlova 2016 [28]; Pavlova and Pitulko 2020 [16], Khlobystin 1998 [39], Mochanov 1977 [109].

Climate changes after ~12.5 ka in the arctic Western Beringia were largely due to the development of the marine Holocene transgression. It proceeded more dynamically at the initial stages up to ~8.3 ka, which led to rapid large-scale flooding of the shelf to the modern −20 m isobath [150]. The highest rates of sea level rise are calculated between 9.8 and 8.9 ka [119]. The development of transgression dynamically changed the outlines of the coastline and actively influenced the increase in the humidity of the climate. Rapid movement of the marine transgression front by ~8.3 ka not only caused an increase in humidity but also had a cooling effect on the environment enforcing an 8.2K event. As a result, the dry continental climate was replaced by an excessively humid marine one, which caused significant cooling and the termination of the development of thermokarst. After ~8.3 ka, the rate of sea level rise slowed down, and the sea level reached its current position at ~5 ka [119].

Archaeological materials that relate to this stage of human settlement in the East Siberian Arctic are few in number (Figure 4). These are, first, the Zhokhov site (Zhokhov Island, New Siberian Islands) (Figure 1H—30), whose excavations brought unique evidence of human adaptation to the conditions of the high-latitude Arctic [149,151]; this site was visited by people repeatedly in the interval of 9.2–8.6 ka [152]. At the time of human presence on the island, it represented the outskirts of the residual area of the former Great

Arctic Plain [20]. It was abandoned after 8.3 ka, when this portion of dry land completely lost its connection to the mainland [117].

The Zhokhov site represents the extreme northern point of distribution of sites, whose contexts contain massive evidence of the use of microprismatic technology for microblade production. The signs of its early presence are known from Taimyr at the Tagenar VI site to Eastern Chukotka seen in the contexts of Chel'kun IV, Naivan, and some others. These sites appear in the region almost simultaneously within the range of ~9 to ~7 ka (Figure 4A) [28,37,39,40,153]. The Zhokhov site settlers hunted reindeer, and in winter, they hunted polar bears (*Ursus maritimus* Phipps) in dens [154]. This is a unique case of mass procurement of polar bears in the world. Excavations of the site also yielded serial finds of morphologically true domestic dog (*Canis familiaris* L.) remains, the earliest in Siberia. A striking feature of this culture is the possession of ground transport technologies—sled dogs and sleds [155]—with whose help they made long journeys. This ability is confirmed by their participation in the system of long-range obsidian exchange from the Anadyr Valley, carried out at a distance of more than 1000 km [156]. The availability of such vehicles ensured high mobility of the population and the rapid spread of technological knowledge.

In addition to these sites, it is necessary to name the dated subsurface contexts of the sites of Podgornaya and Tytyl' IV in the Tytyl' sites group [38] located near Lake Tytyl' in the valley of the Tytyl'vaam River, the right tributary of the Malyi Anyui in its upper course, Western Chukotka (Figure 1H—28; Figure 4A). In the materials of these sites, wedge-shaped core-based splitting occurs, and this is, at present, the oldest dated reliable context of this kind in the Arctic zone at ~11.2 ka.

5. Paleodemography of the East Siberian Arctic in the Late Pleistocene and Early Holocene

Sharp changes in the material culture of the ancient population of the Arctic of Eastern Siberia are associated with both natural and climatic changes as well as the influx of new populations to these territories (Figures 1 and 5). Anthropological remains from the Pleistocene age in Siberia are very rare [157], and in the Arctic, they are isolated (Figure 1J). Materials from the Eurasian Arctic and the Sub-Arctic indicate that the population, which dominated the northern edge of the continent approximately 50,000–45,000 years ago, was physically represented by anatomically modern humans. Thus, the age of a human femur found near Ust-Ishim, at 57° N, was approximately 45,000 years ago [158]. In the genetic sense, the find belongs to a representative of the ancient population of Northern Eurasia, who occupied this territory on the eve of the major split between Western (European) and Eastern (Asian) lineages of modern people [158], with a slight admixture of a Neanderthal genome absorbed by them much earlier than 45,000 years ago and observed at the same level in the genomes of today's Europeans.

In addition to the Ust-Ishim man, only the findings of human milk teeth from the Yana site are known in the north of the continent [67,159]. The preservation of DNA in two of them made it possible to sequence the genome of the inhabitants of the Yana site with high resolution [67]. It has been established that the population to which the Yana people belonged replaced the undifferentiated Ust-Ishim population in northern Siberia (Figure 5).

This group, called the "Ancient North Siberians" (ANS), separated from the European line approximately 38,000 years ago, shortly after the divergence of the major split that happened approximately 43,000 years ago. ANS likely separated from the West Eurasian lineage; however, their genome kept, at the same time, a significant (up to 30%) East Asian admixture that is associated both with common ancestors and close geographical proximity, as well as the proximity of events in time.

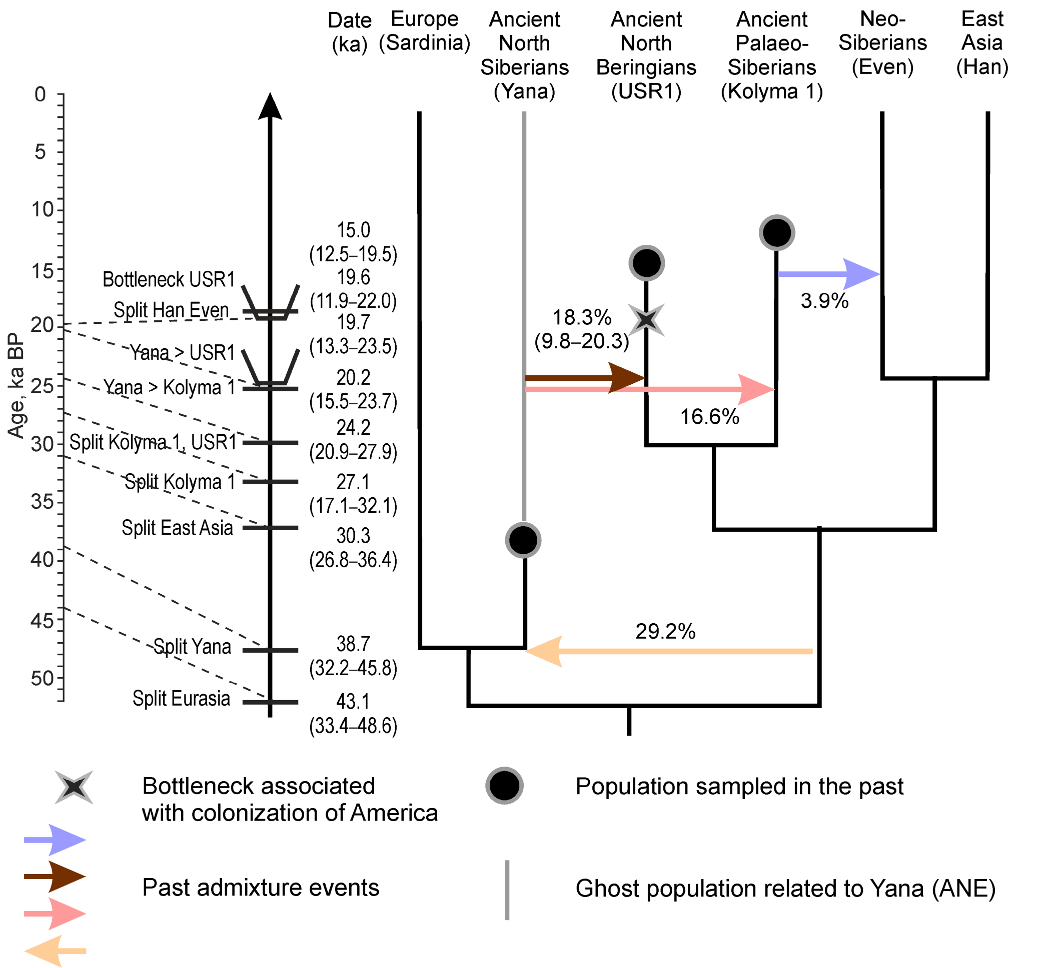

Figure 5. Demographic modeling for Siberian and North American ancient native population: Identified patterns, the time of event (in thousand years ago), and assessment of connection of various genetic lineages (in percent) (after Sikora et al., 2019 [62]).

During MIS 3 and MIS 2, the population of the East Siberian Arctic was most likely represented by the ANS population, to which the inhabitants of the Yana site also belonged [67]. These people made a significant contribution to the formation of the ancient Beringian population that colonized the New World but did not participate in it directly. It was formed as a result of the unification of the ancient local genetic lineage of the North Siberian population and a powerful genetic impulse of East Asian origin, which moved northward following the deterioration of natural and climatic conditions in the interior of the continent during the LGM [160,161]. The genetic characteristics of migrants who displaced or assimilated the Ancient North Siberians are known, thanks to the discovery of an incomplete human skull on the lower reaches of the Kolyma River in the well-known Duvannyi Yar exposure [159]. The find is ~10,000 years old and marks the complete replacement of the former inhabitants of the territory by the bearers of genomes of the East Asian lineage [67].

6. Adaptations of the Arctic East Siberian Population in the Late Pleistocene and Early Holocene

Based on the listed materials, it can be seen that people who entered the East Siberian Arctic around 50,000 years ago have never left it, although, at certain intervals, they experienced demographic stress seen as the bottle-necks in the genetic record, during the LGM and near the Pleistocene/Holocene boundary. Since the early stage of human penetration in the area, the territory has been widely inhabited [162]. A significant contribution to the historical and cultural development of the territory was made by migrations in a south-to-north direction associated with the movement of carriers of the genomes of the East Asian lineage (Figure 5). The reason for these movements of the human population is the frontier of natural and climatic changes of the Late Pleistocene–Early Holocene (Figure 1).

One of the most important cultural and economic characteristics of the epoch is 'human–mammoth' relationships. Throughout the entire period of the joint existence of humans and mammoths, these animals remained the object of the hunt, as is attested by direct evidence observed on the bone remains of woolly mammoths, for example, found in a number of sites, such as Sopochnaya Karga, YMAM locality in the Yana complex of sites, Tabayuryakh, Wrangel Island, Ilin–Syalakh 034, and Nikita Lake. They are present in all time slices, which is supported by the evidence of the existence of the production technology of long points from mammoth tusks, contemporary to them.

Many of the locations of the early and middle stages of settlement (at least 11 of them) are associated with massive accumulations of mammoth bone remains. On the basis of materials in the Upper Paleolithic of Northeast Europe, there was previously the opinion [163] that the people of this epoch exploited the "graveyards" of mammoths, that is, natural mass concentrations of their bone remains, in connection with which there was a specific localization of the sites of ancient man, confined to such clusters. Materials from the East Siberian Arctic show that this is not the case. Such concentrations have an anthropogenic nature and arise as a result of human hunting of these animals, which leads to the formation of "warehouses" (stocks of biogenic raw materials, primarily osseous materials).

The nutritional value of this animal, most likely, was limited since these people extracted animals of other species of fauna from the Late Pleistocene in multitude: Pleistocene bison, horse, reindeer, hare, and predators: Bear, wolf, arctic fox, and wolverine. The use of these animals is typical for the entire Late Pleistocene, but at the turn of the Holocene, the resource base had been reduced to reindeer and elk (*Alces alces* L.), and possibly musk ox, and therefore exotic resources had also been used, for example, polar bear in the areas of maternity dens [154]. There are no early Holocene traces of marine adaptations (hunting of sea mammals and fishing) in the culture of the population of the East Siberian Arctic for MIS 3 and MIS 2 since there was no environment in which it was possible: The formation of the marine ecosystem of the shelf zone of the Eastern Arctic began after 9000 years ago following the flooding of the coastal plains and the opening of Bering Strait, and continued until the middle of the Holocene.

In terms of the development of the lithic industry, there are fundamental differences between the sites of various stages, coinciding in time with the main climatic boundaries (Figure 1A–I). So, for the early stage, the presence of a flake industry of archaic appearance is characteristic, based on the splitting of pebbles and preserving some Middle Paleolithic elements, even the idea of splitting based on a simplified (opportunistic) scheme; these features are present in the Yana site industry in the final segment of the early stage of the human settlement of the arctic east Siberia. However, there is no reason to think that it was preceded by some advanced variant of technology with the production of blades. The materials of the LGM locations are characterized only by the actual evidence of human presence, which at that moment was weak. The only object that contained stone artifacts of this time enables one to think that in the East Siberian Arctic at this time, the industry of small blades was spreading, for which cores with a circular removal system were used. At the end of this stage, the technology of end-wedge-shaped core splitting appears in the region, present in rare sites of this stage in Western Chukotka and, possibly, in the northern Yana-Indighirka lowland.

The successful mammoth population of Eastern Siberia, which was widespread within its borders, experienced a noticeable decline in the number during the end segment of MIS 3, and during the LGM, it decreased even more. The described features of its spatial dynamics [54] suggest that it was shrinking in a northerly direction. It is noteworthy that a new technology of stone processing (wedge-shaped core-based microblade technology) was spreading in the same direction (to the north and east) from the regions of Northern China and Mongolia adjacent to Western Beringia.

The spread of this lithic technology is most likely due to the migration of the population from the inland region, faced with a sharp cooling and aridization of the climate due to the manifestation of the global climatic trend during the LGM (Figure 1B), with a decrease in the average global temperature by 8 to 9 °C [164]. This process was reinforced by the increase in the dry land surface area in North Eurasia due to the decrease in ocean level, thanks to which the coastline in the LGM shifted more than 1000 km north of its current position [136].

The consequence of these events was the desertification of the intracontinental area [160,161], migration in the northern direction of the boundaries of vegetation zones, changing landscapes, and spatial redistribution of populations of fauna that served as a resource base for the population of these areas. In fact, the very appearance of microblade production technology based on wedge-shaped cores is most likely a consequence of environmental and climate change and is associated with the fall-out of mammoth from the biome of the southern part of the tundra-steppe of Northern Eurasia since tusks served as an important raw material for the production of hunting equipment—long points and/or full-size spears of mammoth tusks [54].

In the terminal Pleistocene, complexes with Chindadn points (small incomplete bifaces of a predominantly teardrop shape) appear in the East Siberian Arctic, which are widespread in Northwest North America (Eastern Beringia); this form represents the only archaeologically visible connection between these territories. At the turn of the Holocene, these differences disappeared, and the lithic technology changed again. Microprismatic blade technology is rapidly spreading across the entire region, from Taimyr to Chukotka and from its southern regions to high latitudes (Figures 1G–I and 5), associated with the settlement of carriers of East Asian genetic lineages in the territory of Eastern Siberia [20,67]. This process was likely accelerated and simplified by the presence of the land transportation system among populations of the early Holocene arctic Siberia in the form of sled dogs and sleds [155]. Their appearance is associated with the completion of the dog/wolf domestication process in the terminal Pleistocene, and thus this land transportation system is the most important innovation in the human culture of the Arctic at the turn of the Holocene [6].

It was thanks to a set of Upper Paleolithic innovations that the Upper Paleolithic people were capable of mastering the boundless open spaces of the mammoth steppe. More precisely, these innovations reflect the technological complexity of the ancient man's culture [165,166]. Each of the innovations from the 'Mellars list' [167] hides a set of hierarchically organized particular technologies, which is easy to imagine using the example of the technology of manufacturing clothing and other products from hides and skins [91]. The main technologies listed by Mellars [167] do not have a hierarchy, but it is obvious that the most important were the actions directly related to the technology of survival of human groups in the open spaces of the tundra-steppe belt of Northern Eurasia. Evidence of such technologies is fully present in the materials of the Yana site.

Initially, three of them are the most significant: Hunting for food, making clothes, and building dwelling structures. The extraction of animals by hunting in all chronological references supplied raw materials for producing products from hides and leather. It also satisfied the need for raw materials for the production of bone products; the most important were hunting weapons and sewing tools.

The garment industry was obviously one of the two critical technologies necessary for human development of the coldest regions of the planet. Its development is associated with the appearance of the eyed needle, the most ancient of which was found in Siberia [168,169]. In Siberia, there are known archaeological sites where mass production and use of such implements in MIS 3 are documented, especially in the Yana complex of sites [91]. The introduction of eyed needles made it possible to produce multi-layered clothing and adjust it to size, as well as to create a full range of sewn products—shoes, sleeping bags, soft containers, and bags—as well as dwellings. The latter, judging by the evidence from excavations of the Yana site, were light ground structures with hearths [89], for which bones of large animals, including mammoths, were used as fuel in winter [88].

The presence of a developed sewing culture is an indispensable condition for successful human activity in the subarctic and Arctic zones, where the current average annual temperatures vary from 0 to −16 °C, and any slight decrease in the global average temperature will significantly worsen environmental conditions. Such changes occurred at different times; the most famous are the LGM and the sharp Younger Dryas cooling. However, sudden short-term cold spells, defined in the climatic record as Greenland stadials, were much more numerous [170]. They undoubtedly contributed to the spatial distribution of human groupings and caused certain changes in the material culture of this population as a cultural response to changes in the habitat.

During MIS 3 and MIS 2, the studied territories of Northern Eurasia were occupied by a tundra-steppe biome (see, for example: [49,148,171]), which differed by significant variability in space and time. The main feature of the natural environment of these landscapes was the complete or almost complete absence of woody vegetation [41,147]. This circumstance was extremely important for ancient man in the Arctic since wood served not only and not so much as fuel but also as a construction material used for the frames of dwellings. Finally, it served as a material for the manufacture of hunting weapons, namely, the shafts of spears and thrown spears.

If in the first two cases, it can be replaced, i.e., to use shrub branches, peat, bones, and animal fat as fuel, and use large shoots of shrubby plants as a building material for dwelling frames, as such shoots can easily reach 3 to 4 m in length in habitats favorable for growth (for example, willow shoots in river valleys), then a much higher quality material is needed to make a spear shaft. As in the case of mastering sewing technologies, which look like everyday ordinary work, with little visibility in the culture, incomparable with the true meaning and role of this technology in adapting to the harsh environment, the use of wood in any situation looks simple and natural [172]. It is possible to fully assess the degree of importance of this resource only if it is completely absent. This is exactly the situation that arose at the time of the initial penetration of people into the open spaces of the tundra-steppe belt of the Eurasian Subarctic and Arctic.

To overcome the lack of wood, an original solution was found. It consisted of the development of a special technology for the longitudinal splitting of mammoth tusks, which helped make it possible to obtain long strong points up to 2 m long, reaching the length of a full-sized spear. Traces of this technology are best documented in the materials of the Yana site [56] and at Berelekh [173], although there are relatively many in the area [56]. In any case, with its help, it was possible to obtain serial long massive points necessary for hunting large Pleistocene herbivores, including mammoths.

Mammoth hunting was an important activity. However, it was carried out on a limited basis with a very low volume (1 to 2 animals per year). It was undoubtedly connected to the need to create a stock of important bone raw material [56,93] and possibly fat, which, along with bones, could have been used as fuel in winter. Meat was used for food, but it did not play a significant role in the diet of the ancient hunters of the Siberian Arctic, who extracted Pleistocene bison, horses, and reindeer in large numbers [93]. There is no evidence of a mass one-time mammoth hunt [3,92,126].

The interaction of "man–mammoth" is a fundamental characteristic of the Late Pleistocene epoch, in connection to issues related to its disappearance as a result of exterminating hunting of it by ancient man often discussed. This issue was studied using the example of the historical dynamics of the population of North Siberian woolly mammoths [75]. The relative size of the mammoth population changed over time, but no anthropogenic contribution is visible in these changes. As was shown earlier [75], such fluctuations in mammoth often exactly repeated changes in the proportion of xerophytic beetles in the entomofauna, which, in turn, are an indicator of the presence of steppe vegetation in the phytocenoses of the late Pleistocene Western Beringia [24,174,175].

After the end of the last glacial maximum, the population of Siberia gradually increased. However, it affected the fate of mammoths to a very small extent. The number of dates for mammoths attributable to the interval from 15,000 years ago to the turn of the Holocene increases rapidly and only then decreases abruptly. The growth of the mammoth population occurs against the background of a simultaneous increase in the human population and its density. Thus, the presence of humans had no noticeable effect on the stable mammoth population.

Changes in the natural environment for a long time affected the mammoth population more than coexistence with man. Their action at the very end of the Pleistocene and Holocene led to the collapse of the mammoth population and their concentration in a narrow northern refugium, which for this species, is a normal strategy of surviving unfavorable climatic epochs. Along with the biological mechanisms of adaptation (the appearance of small forms), such a strategy could have worked this time but did not. The final extinction of mammoths, in fact, occurred due to their interaction with humans in a limited space occupied by a small population, and this means not only the direct extermination of mammoths by humans. It is possible that for the disappearance of the remnants of an oppressed isolated mammoth population, it was enough just to have a joint presence in the same territory with people. In a certain sense, their disappearance is a consequence of the successful adaptation of the ancient inhabitants of the East Siberian Arctic to the conditions of the environment.

7. Conclusions

The existing archaeological chronicle of the Stone Age of the East Siberian Arctic covers approximately 50,000 years, from the early phase of MIS 3 (late Pleistocene) to the Early Holocene (beginning of MIS 1). These data are not numerous; however, three chronological groupings can be confidently distinguished: (1) Early (~50 to ~29 ka, MIS 3); (2) Middle (~29 to ~11.7 ka, MIS 2), and (3) Late stage (Early Holocene, from 11.7 to ~8 ka). In the Early Stage, flake-based lithic technology of archaic appearance using a variety of local rocks was widespread; in the Middle Stage, lithic technology based on wedge-shaped core splitting (the Beringian microblad tradition) spread into the Arctic zone, and its appearance in the Arctic regions follows the reduction in the range of woolly mammoths of Eastern Siberia during the LGM. During the Early and Middle stages, the flake-based lithic industries were accompanied by the technology of manufacturing long points from a mammoth tusk. With the reduction in the number of mammoths and the gradual loss of the source of that biogenic raw material, this technology was replaced by the production of grooved tools, initially realized through the production of microblades in the framework of end-wedge-shaped core technology, with a subsequent transition to microprismatic splitting. In the late stage, from the turn of the Holocene to its middle, in Arctic Beringia, variations in lithic industries with microprismatic core-based splitting spread. The connection of the archaeological material with massive accumulations of mammoth bone remains, which are man-made objects formed as a result of human exploitation of the local woolly mammoth population at that time, is clearly manifested. Archaeological materials allow us to reconstruct the human dispersal and adaptation to the Late Pleistocene and Early Holocene to the conditions of the natural environment.

The Arctic region of Eastern Siberia, starting from the moment of initial human exploration shortly after 50,000 years ago, has continuously remained inhabited by human populations, including the least favorable periods that are difficult from the point of view of natural and climatic conditions. Cardinal changes in archaeological cultures and technologies correspond to the most important paleoclimatic boundaries of the Late Pleistocene and Early Holocene. In all cases, they are associated with migration to the Arctic region of the southern population belonging to the East Asian lineages with the exception of the initial stage of development of the territory associated with the settlement of carriers of the Western Eurasian gene pool. These changes should be considered a form of feedback connection—the adaptation of Stone Age hunters to the conditions of their habitat.

During the Late Pleistocene, the population of the East Siberian Arctic carried out economic activities within the framework of the model of continental hunters who exploited all available resources in the form of local populations of Pleistocene fauna, among which Pleistocene bison and horses, as well as reindeer, were the most important as food resources, while the mammoth served primarily as a source for raw material (tusks, bones, and fat). At the turn of the Holocene, species diversity was reduced to a state close to modern. In the Arctic zone, reindeer became the main source of human existence, but exotic resources were also used, for example, the polar bear in the early Holocene on Zhokhov Island.

The condition for the initial development of Arctic territories and the successful life of people of the Stone Age of the Late Pleistocene in a changing natural environment was the introduction into economic practice of important technological innovations—comprehensive/complex technologies. In the adaptations of the Late Pleistocene, an important role was played by technologies for the production of hunting equipment (long points and full-sized spears) from a mammoth tusk and advanced sewing technologies based on using the eyed needles, the use of which was crucially important. The most important innovation at the turn of the Holocene was the completion of dog/wolf domestication, the formation of a breed of sled dogs that served as the genetic source of all currently existing sled breeds, and the creation of land-based transportation resources (sled dog teams). This achievement ensured the mobility of the population at the turn of the Holocene and contributed to the rapid dissemination of cultural knowledge and population exchange. This innovation ensured the emergence of large socio-cultural systems, whose spatial expression reaches millions of square kilometers.

Settlement of the Eastern Siberian Arctic of the Late Pleistocene is associated with the initial settlement in the region of people whose genome is dominated by the Western Eurasian lineage. A significant contribution to the historical and cultural development of the territory was made by human migrations in a south–north direction associated with the relocation of carriers of the genomes of the East Asian lineage. The reasons for these relocations of the human population were the milestones of the natural and climatic changes of the Late Pleistocene–Early Holocene.

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