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The characteristics of a relic steppe of Northeast Asia: refuges of the Pleistocene Mammoth steppe (an example from the Lower Kolyma area)

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Abstract. An ecosystem of a relic petrophytic steppe was studied in the Lower Kolyma River region. The soils of the steppe area significantly differed from those of the surrounding open larch forests in the following features: the presence of humus-accumulative horizons with a high content of roots; low moisture content; high heat supply; an extremely contrasting temperature regime; neutral reaction; decreased potential acidity; higher humification of organic matter; accumulation of exchangeable bases, soluble salts and organic nitrogen; and the presence of carbonate neof ormations in the form of cutans on pebbly units. They also had a high microorganism saturation of the soil profile, a high share of actinomycetes in the microbial community, as is typical for arid soils, and a shift in the ratio of potential enzyme activities toward oxidoreductases, which reflects a deeper destruction of plant residues and more intensive humus formation. The petrophytic steppe had high bioproductivity. The growth rate of the aboveground phytomass (ANP) was closer to the true steppes of Central Asia than to the zonal tundras of the Arctic and Subarctic; such communities can serve as models for paleoreconstructions and study of the Late Pleistocene cold steppes - mammoth fauna large grazing mammals habitats.

1. Introduction

In the Late Pleistocene, cold steppes (so-called tundra-steppe, steppe-tundra or mammoth steppe) were widespread in northeast Asia (western Beringia) and northwestern North America (eastern Beringia). These were living environments for mammoth fauna, mainly large grazing mammals, such as: *Mammuthus primigenius* (Blum.), *Coelodonta antiquitatis* (Blum.), *Equus* spp., *Bison priscus* Boj., *Ovibos pallantis* H. Smith, *Saiga tatarica* L., and others. Paleontological data indicate that about 40 species of large mammals inhabited Pleistocene pastures at high latitudes. The species diversity of megafauna in the northern Holarctic was significantly higher than at present, and was comparable to the current diversity of ungulates in East Africa [1, 2]. This paradoxical phenomenon indicates the high productivity of the mammoth steppe, which consisted of mosaic landscapes dominated by grass



and herb communities with some shrub tundra and forest areas [1, 2]. The high sustaining capacity of the environment, ensuring a significant population density of large phytophages, can be indirectly confirmed by the high frequency of skeletal remains of megafauna species in the permafrost. According to Zimov's calculations, the biomass of mammoth fauna mammals in northern Siberia could have reached $\sim 10 \text{ t/km}^2$, which is comparable to the biomass of modern large ungulates in the African savanna [3] and cattle in the South American Llanos [4].

Climate warming at the boundary between the Pleistocene and Holocene resulted in the displacement of vast steppe areas by tundra and taiga in the major part of northeast Asia. The modern Arctic is dominated by various tundras, which cannot maintain the high diversity of grazing mammals [1, 2].

At present, small areas (of several square meters to a few hectares) of extrazonal steppe vegetation remain on the southern slopes of riverbanks and elevations in western and eastern Beringia, with high insolation and low snow cover. Many authors consider these areas relics of the Pleistocene mammoth steppe [2, 5-10]. The presence of the steppe areas is due to the local combination of hydrothermal conditions which are favourable for the development of grass communities under strongly continental semiarid climate conditions.

The relic steppe ecosystems of northeast Asia and northwestern North America are valuable sources of information about the cold Pleistocene tundra-steppes and they need a comprehensive study. Integrated studies of their properties can play a key role in the elucidation of important paleoecological issues, such as the fertility and productivity of tundra-steppe soils, which formed a basis of subsistence for the mammoth biome, and some paleogeographical problems.

Our studies were performed in the northern Kolyma Lowland near Chersky Village, Republic of Sakha (Yakutia), where steppe slopes were repeatedly described by different authors [11-16]. The work was aimed at studying the main components of the petrophytic steppe ecosystem and assessing the productivity of its plant associations.

2. Study region

The lower course of the Kolyma River belongs to the Kolyma Lowland, which is an accumulative plain composed of thick loose Tertiary and Quaternary deposits. The study area is located on the Kolyma River right bank in the low course, not far from the western spurs of the Anyui Ridge with absolute marks up to 650 m [17]. Exposed rocks are frequently covered by an ice-rich silty-loamy sediments of the Late Pleistocene Yedoma Suite (Ice Complex) [18] or products of their Holocene transformation. In this area, Late Pleistocene deposits contain significant amounts of mammoth fauna remains [19-22].

The Kolyma Lowland is underlain by continuous permafrost, which is the oldest underground ice formation of Eurasia since the Pliocene [18]. The mean annual temperature of permafrost in the region varies from -3 to -6 °C for the Yedoma uplands and from -5 to -8 °C for the floodplains. The active layer thickness varies from 0.15 to 1.80 m, but the average depth of seasonal thawing does not exceed 1 m.

The region belongs to the sub-arctic belt of the continental climate area, with a long cold winter and a short cool summer [23]. At the Chersky meteorological station data, the mean annual air temperature varies from -10.5 to -7.3 °C. The long-term mean temperature is -32.3 °C for the coldest month (January) and $+13.1$ °C for the warmest month (July). The maximum difference between the mean temperatures in January and July is 45.4 °C. The period of positive mean daily temperatures lasts 115–145 days, and the number of days with the mean daily air temperature above 10 °C is 57. The sum of temperatures above 10 °C is 819 °C. The climate is temperate dry, and annual precipitation is 171–322 mm.

The region belongs to the band of pre-tundra open forests in the northern taiga subzone. The landscape is dominated by pre-tundra sparse larch (*Larix cajanderi* Mayr.) forests. The grass layer is poorly developed [24]. The soil cover of taiga landscapes has a complex structure. Cryometamorphic

soils (Cambic Turbic Cryosols) occupy the better-drained positions, and cryozems (Turbic Cryosols) occupy the worse-drained positions.

3. Objects of study

The study petrophytic steppes are located on steep slopes of the Panteleikha River right bank, where hard rocks are exposed on the surface (figure 1).

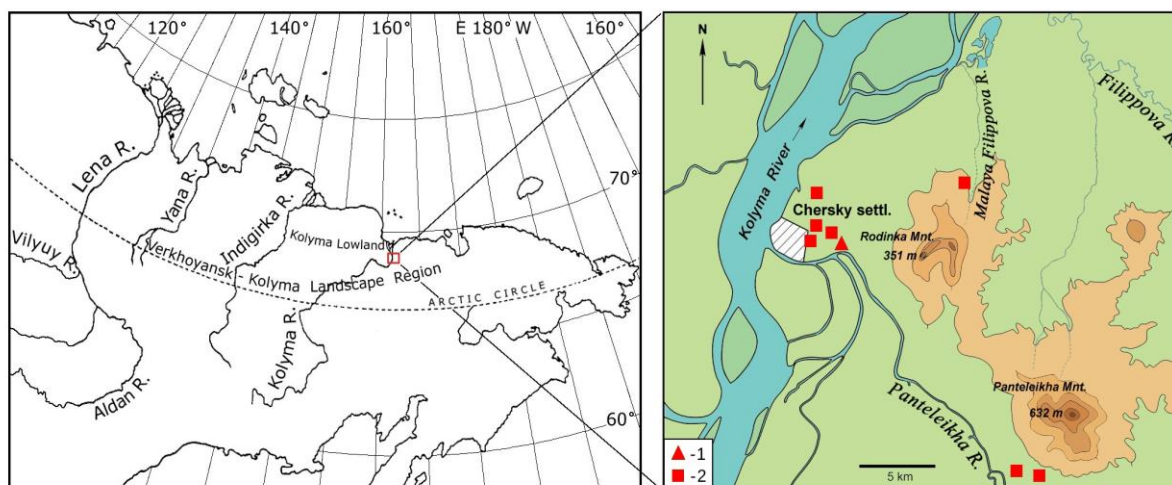


Figure 1. Region of study: (1) key plot of petrophytic steppe; (2) locations of soil profiles in sparse larch forests.

The sizes of petrophytic steppes vary from several square metres to a few hectares. The steppe vegetation includes different versions of herbaceous communities with the participation of grasses *Festuca kolymensis* Drobov, *F. jacutica* Drobov, *Calamagrostis purpurascens* R. Br., sedges *Carex pediformis* C.A. Mey, *C. rupestris* All. The abundance and share of herb species *Pulsatilla multifidi* (G. Pritz.) Juz., *Phlox sibirica* L., *Silene stenophylla* Ledeb., *Pedicularis venusta* Schang. ex Bunge, *Thymus diversifolius* Klok., *Potentilla arenosa* (Turcz.), *Arenaria tschuktschorum* Regel, *Dianthus versicolor* Fisch. ex Link., *Galium verum* L., *Veronica incana* L., and *Dracocephalum palmatum* Stephan are not constant and depend on the weather conditions of the growing seasons. The species *Lathyrus pilosus* Cham., *Sedum aizoon* L., *Allium strictum* Schrad., *Carex rupestris* All., *Poa attenuate* Trin., *Galium boreale* L., *Lactuca sibirica* (L.) Maxim., *Tanacetum vulgare* L., *Lychnis sibirica* L., *Elytrigia jacutorum* (Nevski) Nevski, *Draba cinerea* Adams, *Thatictrum contortum* L. insignificantly contribute to the formation of phytoceneses in the petrophytic steppe, although they can be an aspect of some plant microgroups, especially during warm and humid years. The total projective grass cover is 50–70%. According to classification based on the Braun-Blanquet approach, these steppe communities are presumably related to still undescribed association *Thymo – Pulsatilletum multifidae* ass. nova of class *Cleistogenetea sguarrosae* Mirk. et al. 1986 ex Koroluk 2002, order *Helictotrichetalia schelliani* Hilbig 2000, alliance *Pulsatillion flavescens* Mirk. in Gogoleva et al. 1987, suballiance *Pulsatillo multifidi – Thymenion pseudoaltaici* Saitov in Pestryakov et al. 1992 [25].

The steppe soils are classified as lithozems (Eutric Leptosols) or organic-accumulative soils (Eutric Epileptic Regosols), depending on the depth of the eluvial-deluvial cover. They frequently contain buried horizons in soil profiles because of intensive slope processes.

The Russian names of the soils correspond to “The Field Guide for Russian Soils” [26]; the corresponding equivalents from the World Reference Base for Soil Resources (WRB) are given in parentheses [27]. The names and indices of soil horizons are given according to the Russian soil classification.

4. Study methods

The temperature regime of the steppe and cryometamorphic taiga soils were studied from 2008 to 2011. Onset HOBO temperature data loggers were used. Soil moisture was determined by the gravimetric method during the warm season. All analyses were performed according to conventional procedures [28-31].

The biological activity of the steppe and taiga soils was studied in 2008, 2009, 2012, 2016 and 2017. Microbial abundance was determined by limiting dilution and solid medium inoculation, and expressed in colony forming units (CFU)/g soil [32]. The enzymatic activity was determined by the conventional methods of soil enzymology: invertase activity was determined by the method described by Khaziev, Agafarova and Gul'ko and expressed in mg glucose/(g soil·hour); protease activity was determined by the Khaziev and Agafarova method and expressed in mg tyrosine/(g soil·24 hours); phosphatase activity was determined by the Khaziev method and expressed in mg phenolphthalein/(g soil·hour); anaerobic hydrogenase activity was determined by the Galstyan method and expressed in mg triphenylformazan/(10 g soil·24 hours); catalase activity was determined by the Galstyan method and expressed in mL O₂/(g soil·min); polyphenol oxidase activity was determined by the Karyagina and Mikhailovskaya method and expressed in mg 1,4-benzoquinone/(10 g soil·hour); the actual cellulose activity of the soils was determined by the Vostrov and Petrova method and expressed in the dry weight loss of cotton fabric [33]. Microbial and enzyme pools in the soil profile were calculated by the Zvyagintsev method [34].

The productivity of the petrophytic steppe was studied in 2016 and 2017. The aboveground net primary production (ANP) of phytocenosis was determined for this purpose. During the vegetation period, the aboveground phytomass was cut in triplicate in test plots (25×25 cm) thrice per season. Small test plots were used because of the small total area of the relic steppe (see above) and to minimise plant cover disturbance, without losing the information value of cuttings.

Then, the aboveground phytomass was separated into fractions: living phytomass (G), plant fall (D) and litter (L), which were dried and weighed. The ANP was calculated from the dynamics of the different fractions of plant material using the minimum estimation method [35].

5. Results and discussion

5.1. Soils of the petrophytic steppe and surrounding sparse forests

5.1.1. Hydrothermal conditions of soils. The soils of the petrophytic steppe were characterised by manifested xeromorphicity in the background of hydromorphic and mesomorphic zonal soils (figure 2). Their moisture content could vary more than three times during the summer period, but it was generally low: 9–22% in organic-accumulative horizons and 5–16% in pebbly mineral horizons. Shallow soil profiles were almost soaked through during abundant rainfalls, but they rapidly lose the received water because of their position in the relief and their low water-retention capacity. In winter, slight ice formation occurred in the upper part of the profile; it mainly forms a horizontal wavy fine-schlieren cryogenic structure in the fine earth and a freeze-dried crust-like cryostructure in pebbly material.

Soil thawing on the stepped slope began 1–3 weeks earlier and is significantly more rapid than in the taiga varieties. In the steppe soil at a depth of 20 cm, the mean summer temperature was 9.7 °C higher and the mean temperature of the warmest month was 10.7 °C higher than in the cryometamorphic soil of the adjacent sparse larch forest. The annual sum of positive mean daily temperatures at this depth for the petrophytic steppe soil was 1180 °C higher than for the taiga variety. 94% of this value corresponded to the mean daily temperatures >5°C, and 73% corresponded to the mean daily temperatures >10 °C. In the cryometamorphic soil, mean daily temperatures >5 °C constituted 35% of the total sum of the positive temperatures, and no mean daily temperatures >10 °C were observed.

In the cold season, steppe soils cool significantly more rapidly than taiga soils because of the low moisture content and the shallow and compact snow cover in the open unforested areas. In the coldest

month, the soil of the steppe area at a depth of 20 cm was 9.5 °C colder than the taiga cryometamorphic soil. Therefore, the studied soils strongly differ in contrast to the temperature regime. According to Dimo [36], steppe soils have an extra continental climate, and taiga soils have a mild climate.

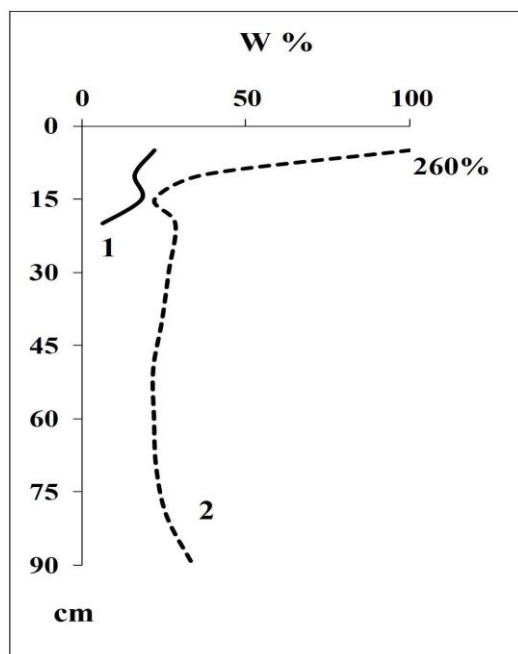


Figure 2. Pre-winter moisture in lithozem of petrophytic steppe (1) and (2) cryometamorphic soil of sparse forest.

5.1.2. Profile structure and chemical status of soils

The taiga soils were characterised by the presence of litter, raw-humus and mucky horizons, for which ignition loss reached 27–52% and the organic carbon content was 20–30%. In the petrophytic steppe, gray-humus (soddy, AY) or mucky–dark-humus (AH) horizons with a significantly lower content of detritus were generally formed in the upper profile part of both lithozems and organic-accumulative soils (figure 3A). Forest soils were characterised by a sharply decreasing accumulative distribution of organic carbon. A smoother decrease of this parameter along the profile is typical for soils of the petrophytic steppe. This situation is due to both the relatively small amount of undecomposed plant residues in the AY and AH horizons and the higher humus content in the middle and lower parts of the profile.

Humus of the studied soils varied in terms of group composition. Cryozems and cryometamorphic soils mainly contained humate-fulvate humus with a medium degree of humification and a relatively high content of nonhydrolyzable residue. In the steppe areas, humus had a fulvate-humate composition in the upper horizons, which generally changed to a humate-fulvate or fulvate type down the profile.

In forest soils, the reaction changed top-down from strongly acidic to weakly alkaline. The content of exchangeable hydrogen (by the Hedroits method) decreased down the profile from 28.11–32.13 to 0.07–0.41 cmol/kg. The degree of SEC saturation increased top-down from 68 to 99%. The steppe soils were characterised by a neutral reaction, low contents of exchangeable hydrogen and a high degree of SEC saturation (88–91%).

The presence of carbonate cutans on the surface of pebble in the Bic horizon (figure 3B), in the absence of fine earth effervescence, indicated the similarity of the studied soils in the petrophytic steppe to the soils in analogous habitats of the upper Kolyma region [9, 37-39].

Calcium or calcium and magnesium were the dominant exchangeable bases. There was a significantly more uniform profile distribution of exchangeable bases and an accumulation of bivalent cations in the mineral horizons in the steppe soils compared to the forest soils.

Ca^{2+} , Mg^{2+} , and HCO_3^- were the dominant ions in the water soil extracts. A tendency towards the accumulation of soluble salts was noted in the steppe soil. The weighted mean of the total salts concentration was 0.034% in the profile of the forest cryometamorphic soil and 0.042% in the steppe lithozem profile.

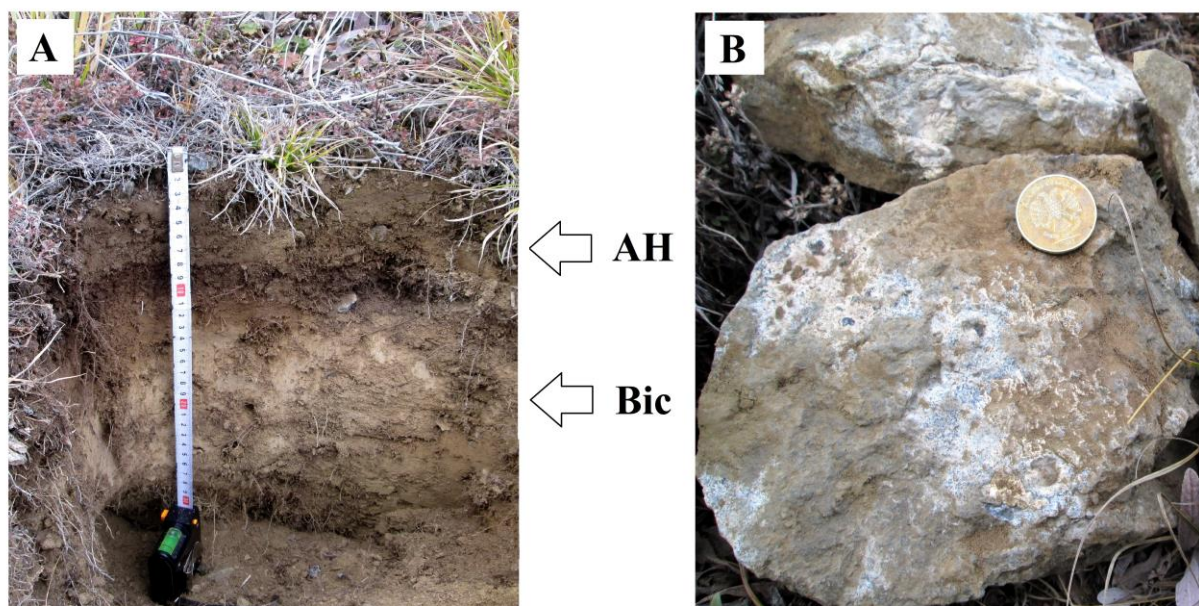


Figure 3. Soil of petrophytic steppe: (A) profile of mucky–dark-humus carbonate coating lithozem; (B) carbonate cutans on the bottom side of pebbly units in the Bic horizon (photo by S.P. Davydov).

Steppe pedogenesis favours the accumulation of nitrogen. The weighted mean total nitrogen content in the mucky–dark-humus soil of the petrophytic steppe exceeded that in the mineral horizons of cryozem and cryometamorphic soil by 2.5 and 3.7 times, respectively. The organic horizons of the taiga soils contained more nitrogen than the soil on the steppe slopes because of the high organic matter content. The concentration ratio of total carbon and nitrogen (C/N) in the upper horizons of the steppe soil (9.4–10.9) was significantly lower than in the upper horizons of the cryozem (38.9) and cryometamorphic soil (22.1–34.0).

Thus, the soils that developed under the petrophytic steppe significantly differed from the adjacent taiga varieties in terms of their profile structure; the decreased actual and potential acidities; the humus content in the mineral horizons; the group composition of the humus; the accumulation of exchangeable bases, soluble salts and nitrogen; the lower total C/N ratio, the increased share of calcium and magnesium ions among the exchangeable bases. The share of calcium and magnesium ions among the exchangeable bases was higher in the steppe soils. Along with the difference in parent rocks, the features of the petrophytic steppe soils were related to their high heat supply, a more intensive biological turnover, the predominant input of litter with grass roots, a low moisture content and an exudation regime hampering the removal of pedogenesis products from the profiles, and intensive winter freezing.

The soils of the petrophytic steppes at the Kolyma Lowland have many features in common with the cryoarid soils described by Volkovintser [40] for more southern Siberia regions and those included in the modern Russian classification [26]. The taxon of Calcic Someric Kastanozems (Cambic) can be considered their analogue in the WRB classification. Along with ecological similarity and analogous hydrothermal regimes, they also share many substantive features, namely: the absence of eluvial-illuvial differentiation of the profile; a granular-powdery or powdery structure; the group composition

of humus; humus distribution and accumulation in the soil; the relatively low total carbon and nitrogen (C/N) ratio; and the presence of carbonate cutans on pebbly units.

5.1.3. Soil biological activity

The biological activity of the petrophytic steppe soil was studied in comparison with cryozems and the cryometamorphic soils of sparse larch forests.

The profile distribution of microorganisms was that of an accumulative character. In the steppe soil profile, the abundance of microorganisms decreased with depth less abruptly than in the soils of sparse forests. The coefficient of differentiation, which is calculated as the ratio between the microbial abundances in the humus AY (AH) horizon and the mineral horizon at a depth of 20–30 cm, was within the range of 3–6 for the soils from steppe areas; between the organic AO (O) and mineral horizons at the same depth in cryozems and cryometamorphic soils, it reached 40–140 for bacteria and 1000 for actinomycetes. This situation is due to the development of more favourable conditions for the active development of microflora in the shallow, pebbly, well-heated and well-aerated soils of the petrophytic steppe than in the cold and wet, frequently thixotropic varieties of forest soils. The humus content, an important source of carbon and energy for microorganisms, was higher in the middle and lower parts of the steppe soil profiles.

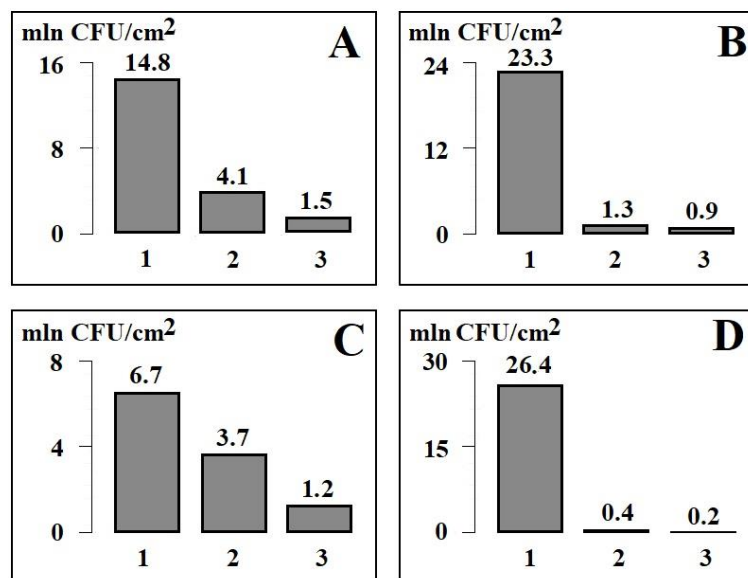


Figure 4. Microbial pools in soil profiles: (1) petrophytic steppe; (2) cryozem, sparse forest; (3) cryometamorphic soil, sparse forest. Microorganisms: (A) bacteria utilizing organic nitrogen sources; (B) oligonitrophylic bacteria; (C) bacteria utilizing mineral nitrogen sources; (D) actinomycetes.

Thus, the relatively high saturation of the soil profile with microorganisms was a peculiar feature of steppe soils; this tendency was even more manifested in the microbial pool calculations, i.e. microbial abundance per unit area. Therefore, the soils of petrophytic steppe had higher values of the microbial pool (figure 4). The bacterial pool that utilises the organic and mineral nitrogen sources in the 30-cm-thick layer of shallow steppe soils was several times larger than in the 50-cm-thick layers of zonal cryometamorphic and cryozem soils. The pool of oligonitrophilic bacteria exceeded that in the cryometamorphic soil and cryozem by tens of times, and the pool of actinomycetes exceeded it by tens and hundreds of times, respectively. According to this parameter, the studied soils form the following decreasing series: petrophytic steppe soils > cryometamorphic soils > cryozems.

Actinomycetes develop actively in steppe soils, in contrast to forest soils. Their abundance reached 7.4 million CFU/g in the gray-humus and mucky-humus horizons (mean value: 2.5 million CFU/g)

and 1.5 million CFU/g in the mineral Bic horizon (mean value: 0.5 million CFU/g). They are predominant among the microorganisms that utilise mineral nitrogen and reach 85% of their total amount. In the pebbly fine-earth layer, actinomycetes were detected down to the dense underlying rock. The high abundance of actinomycetes in the soil layer is a characteristic feature of steppe biogeocenoses [41]. On the other hand, the lower litter layers and humus-accumulative horizons form the main habitation zone of actinomycetes in forest soils. In cryometamorphic soils and cryozems, the abundance of actinomycetes revealed on SAA was significantly lower than in steppe soils (0.75 million CFU/g, on average) and confined to the upper organic horizon only. The deeper transformation of organic matter in steppe soils is also related to actinomycetes activity [42].

There were also some differences in terms of the enzyme complex of the studied soils. A higher dehydrogenase activity was recorded in soils under the petrophytic steppe. In the humus AY and AH horizons, the activity of hydrogenase was 5.57 ± 1.03 mg TPP·10 g/24 h, which was 1.5 times higher than in the organic horizons of the forest soils. Cryometamorphic soils and cryozems had an increased activity of hydrolases (invertase, phosphatase, protease) and the redox enzyme catalase. The activities of these enzymes were 7.75 ± 1.69 glucose·g/h, 42.79 ± 20.74 mg PP·g/h, 3.98 ± 1.43 mg tyrosine·g/24 h, and 8.80 ± 0.99 ml O₂·g/h, respectively; these values exceeded those in the steppe soil by 2.5–3.5 times, and the revealed differences were statistically significant.

A similar situation was observed for the calculation of enzyme pools in the above three soils (figure 5). The pools of redox enzymes dehydrogenase and polyphenol oxidase were relatively large in steppe mucky-dark-humus soil; the pools of hydrolytic enzymes (invertase, phosphatase, protease) and redox enzyme catalase were large in the cryomorph soil and cryozem.

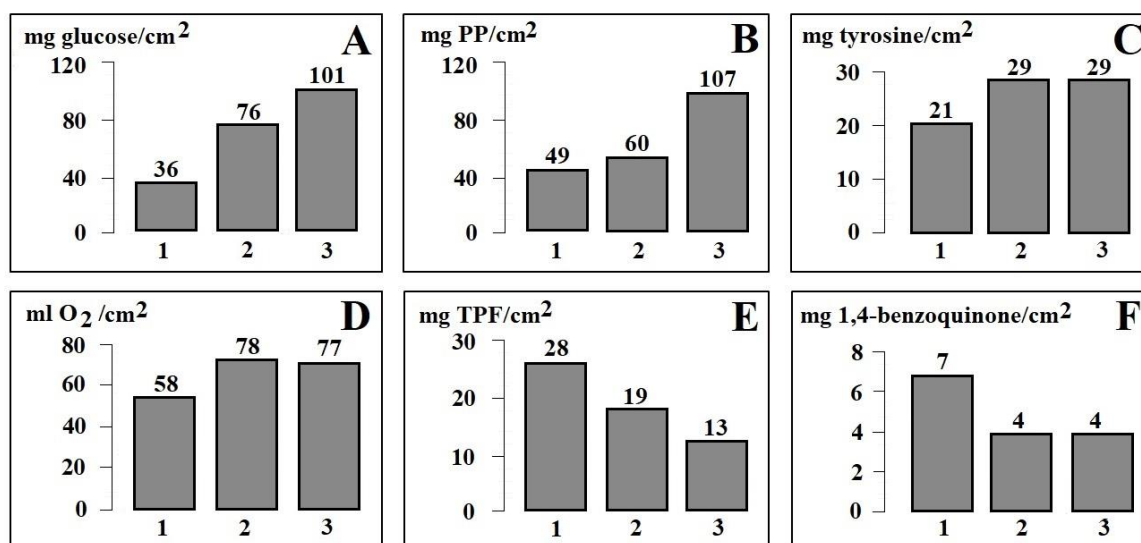


Figure 5. Enzyme pools in soil profiles: (1) petrophytic steppe; (2) cryozem, sparse forest; (3) cryometamorphic soil, sparse forest. Enzymes: (A) invertase; (B) phosphatase; (C) protease; (D) catalase; (E) dehydrogenase; (F) polyphenol oxidase.

The dominance of hydrolases in the enzyme complex indicates that the initial destruction of plant residues occurs in the organic horizons of the cryometamorphic soils and cryozems. The transformation of organic compounds and the formation of humus are more active processes in petrophytic steppe soils with highly dry conditions, good drainage, deep thawing and the development of vigorous roots of meadow-steppe plants. This was confirmed by the organic matter characteristics in the steppe soils: the higher the C/N ratio, the higher the humic acids content and the lower the nonhydrolysable residue content in humus.

Dehydrogenases are known to be present in all living microbial cells, where they determine microbiological redox processes. It is important that dehydrogenases, in contrast to hydrolytic enzymes, not be accumulated extracellularly in soils; therefore, their activity is considered an adequate indicator of the metabolic activity of microflora [43, 44]. This is indirectly confirmed by the direct proportionality between the dehydrogenase activity in the studied soils and the degradation rate of cellulose under natural conditions. In the steppe zone, the degradation rate of cellulose is almost double that in the cryometamorphic soils and cryozems; up to 58% of cotton fabric is degraded after two years in steppe soil, and only 35% is degraded in forest soils.

The literature notes that the activity ratio of oxidoreductases to hydrolases reflects the moisture conditions of the soil formation. Oxidoreductase-catalysed redox reactions are more active under drought conditions, and hydrolytic reactions activated by hydrolases are more active under wet conditions. The increased activity of the hydrogenases recorded in the petrophytic steppe soils reflects the aridity of these soils, which agrees with published data [45].

Thus, the petrophytic steppe soils in the lower Kolyma course are characterised by a higher potential and actual biological activity than the zonal soils of the northern taiga. Their profile is more strongly enriched with microorganisms, among which actinomycetes play an important role. In the steppe soils, the transformation of organic matter is deeper due to the active participation of the redox enzymes dehydrogenase and polyphenol oxidase.

6. Productivity of petrophytic steppe

The vegetation of the petrophytic steppe consists of herbs, in addition to grasses and sedges (figure 6).

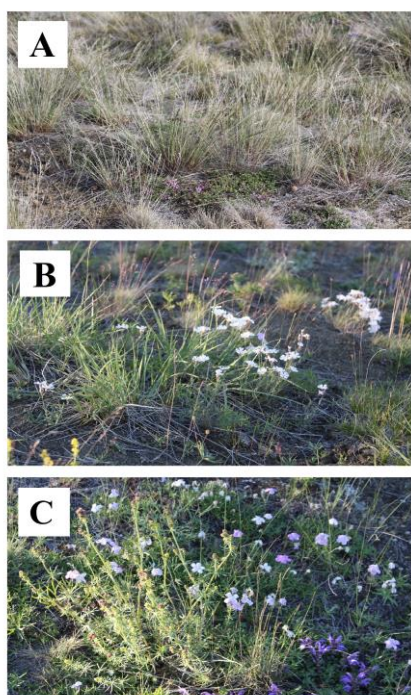


Figure 6. Petrophytic steppe: (A) *Thymo–Pulsatilletum multifidae* ges. *Calamagrostis purpurascens*; (B) *Thymo–Pulsatilletum multifidae* ges. *Pulsatilla multifida*; (C) *Thymo–Pulsatilletum multifidae* ges. *Phlox sibirica* (photo by S.P. Davydov).

In 2016 and 2017, we studied the productivity of the petrophytic steppe by determining the ANP value. This is an essential ecosystem parameter that reflects the amount of chemical energy available for terrestrial heterotrophic organisms, primarily grazing animals. We determined ANP as the growth rate of vascular plants in the aboveground part of phytocenosis and expressed it in grams of dry matter/m² for vegetation season. The productivity has been studied in four communities of *Thymo–Pulsatilletum multifidae* (table 1).

Table 1. Productivity of the extrazonal petrophytic steppe in the lower Kolyma River region, g/(m²·season)

2016 year		
<i>Thymo–Pulsatilletum multifidae</i> ges. <i>Calamagrostis purpurascens</i>	<i>Thymo–Pulsatilletum multifidae</i> ges. <i>Pedicularis venusta</i>	<i>Thymo–Pulsatilletum multifidae</i> ges. <i>Phlox sibirica</i>
278	173	276
2017 year		
<i>Thymo–Pulsatilletum multifidae</i> ges. <i>Calamagrostis purpurascens</i>	<i>Thymo–Pulsatilletum multifidae</i> ges. <i>Pulsatilla multifida</i>	<i>Thymo–Pulsatilletum multifidae</i> ges. <i>Phlox sibirica</i>
104	220	262
arithmetic mean for 2016-2017		
<i>Thymo–Pulsatilletum multifidae</i>		
218.8		

Table 2. Productivity of tundra and steppe ecosystems of Asia

Ecosystem	Study region	P, g / (m ² ·year or season)	<u>X/lim</u>
Arctic tundra	New Siberian Islands, n=2	57	<u>65.5</u>
	Tiksi Bay, n=3	74	57-74
Subarctic typical tundra	Taimyr Peninsula, n=7	93	<u>152</u>
	Taimyr Peninsula, n=9	211	93-211
Subarctic southern tundra	Taimyr Peninsula, n=3	302	<u>156</u>
	Kolyma Lowland, n=2	108	105-302
	Chukotka Peninsula, n=1	110	
Extrazonal petrophytic steppe	Koryak Highlands, n=2	105	
	Lower Kolyma region, n=2	218.8	<u>218.8</u> 195.3-242.3
Meadow steppes	Tyva, n= 1	180	<u>268</u>
	Transbaikalia, n=1	310	180-315
	Mongolia, n=1	315	
True steppes	Khakasia, n=3	360	<u>232</u>
	Transbaikalia, n=5	165	165-360
	Inner Mongolia (China), n=2	170	
Dry steppes	Tyva, n=1	125	<u>128</u>
	Mongolia, n=1	131	125-131

Notes: P – Productivity of aboveground part of phytocenosis, X – mean, lim – limits of the feature variation (min – max), n – number of samples studied.

The results showed that the production process was most active in the *Thymo–Pulsatilletum multifidae* ges. *Phlox sibirica* (table 1). The annual ANP was 276 g/(m²·season) in 2016 and 262 g/(m²·season) in 2017. The ANP of *Thymo–Pulsatilletum multifidae* ges. *Pulsatilla multifida* was lower: 220 g/(m²·season). The *Thymo–Pulsatilletum multifidae* ges. *Pedicularis venusta* had an even lower growth rate of plant material: 173 g/(m²·season). The productivity of *Thymo–Pulsatilletum multifidae* ges. *Calamagrostis purpurascens* strongly varied between the years: it was 278 g/(m²·season) in 2016 and only 104 g/(m²·season) in 2017. In 2016, an extremely humid year, the ANP in the studied community was higher than in 2017, the drier year. The abrupt decrease in the ANP of this community in 2017 was due to not only the worse wet conditions, but also the features of the discount area, with a low projective cover of plants (40%). The average ANP value in the petrophytic steppe, calculated as an arithmetic mean, was 242.3 g/(m²·season) for 2016 and 195.3 g/(m²·season) for 2017; the arithmetic mean for the two years of study was 218.8 g/(m²·season).

The productivity of the extrazonal petrophytic steppe in the lower Kolyma River region was compared to the productivity of Asiatic zonal tundras and steppes. We compared the average growth rates of the aboveground part of plant communities in arctic and subarctic tundras [46] with those in dry, true, and meadow steppes [47] (table 2).

The activity of production process in the zonal ecosystems of tundras and steppes regularly changes in the latitudinal direction, according to the heat and moisture input to the land surface.

The productivity of aboveground biomass in the tundra increases when going from arctic tundras to southern tundras; this is due to the rise in mean annual temperature and the extension of the vegetation season in the true and southern tundra subzone. According to average estimates, productivity in the Arctic tundras of Northeast Asia varies from 57 to 74 g/(m²·year), with a mean value of 65.5 g/(m²·year) [46]. Similar results were obtained for the ANP of coastal arctic tundras in Alaska and the Yukon. Johnson and Kelley [48] found that the ANP of cotton-grass tundras was 82 g/(m²·year). According to Bliss [49], the ANP (aboveground + underground) value varies in the range of 50 to 100 g/(m²·year), with maximum values of 190 to 226 g/(m²·year) in wet sites. The productivity of the underground part of phytocenosis in tundras exceeds the productivity of its aboveground part by 1.5 times, on average; therefore, it should be expected that the ANP of arctic tundras is 20–40 g/(m²·year), with a maximum value of 90 g/(m²·year).

At lower latitudes, the productivity of tundra ecosystems increases. In typical subarctic tundras (Taimyr Peninsula), productivity varies from 131 to 248 g/(m²·year), with a mean value of 153 g/(m²·year). In southern tundras, the growth rate of the aboveground biomass varies from 86 to 302 g/(m²·year), with a mean value of 156 g/(m²·year) (table 1) [46].

In the steppe zone of Central Asia, productivity decreases from meadow steppes to true and southern steppes in accordance with increasing climate aridity. The ANP of the Asiatic reserved meadow steppes in Transbaikalia (Russia), Mongolia and Tyva (Russia) are 310, 315 and 180 g/(m²·year), respectively, with a mean value of 268 g/(m²·year). In the true steppes, where grazing is prevented, the ANP varies from 165 g/(m²·year) in Transbaikalia and 170 g/(m²·year) in Inner Mongolia (China) to 360 g/(m²·year) in Khakasia (Russia), with a mean value of 232 g/(m²·year). In dry steppes, the ANP is 128 g/(m²·year) in Tyva and 131 g/(m²·year) in Mongolia [47].

The productivity of the extrazonal petrophytic steppe in the Lower Kolyma region (218 g/(m²·year) is an intermediate value, between that of the southern tundras (156 g/(m²·year) and the true steppes (232 g/(m²·year). Although slightly different methods were used for ANP determination, in the first approximation, the activity of the production process in the petrophytic steppe is similar to that in the true steppes of Central Asia.

The extrazonal petrophytic steppes of the Lower Kolyma region occur within the pre-tundra thin forests; they are characterised by a high productivity of plants, compared to the adjacent tundra ecosystems. On the well-heated southern slopes of the Panteleikha River valley side, they receive more heat than the surrounding landscapes, which increases the ANP of plants. The rise of the soil temperature, the extension of vegetation season and the oxidative conditions in the soil activate the biological and biochemical decomposition of soil organic matter, enhance biogeochemical turnover

and increase the availability of mineral nutrients to plants in the petrophytic steppe; this accelerates the growth of plants. The positive effect of higher temperatures on the decomposition of soil organic matter and the primary productivity of the ecosystem has been demonstrated for many northern biogeocenoses [50-53]. Along with the above features, the extension of the photosynthesis period due to the longer duration of solar light at high latitudes is an important factor that increases the productivity of the petrophytic steppe. Calculations show that, in the studied steppe area (near Chersky Village, 68°45' N, 161°19' E), the duration of solar light during the warm period (May-September) is higher than in the true steppes of Transbaikalia (city of Chita, 52°01' N, 113°30' E) by 648 hours. The high-latitude extrazonal steppes receive the maximum heat during the same period, which increases the production rate to a level close to that in the zonal steppes. Mordkovich [54] emphasised the important role of the duration of solar light for the functioning of steppe vegetation; Guthrie [2] considered it one of the key factors for the formation of highly productive Pleistocene mammoth steppes.

7. Conclusions

The studied extrazonal petrophytic steppe ecosystem, which is located on the steep southern slope of the Panteleikha River within the pre-tundra sparse larch forests of the Kolyma Lowland, significantly differs from the ecosystems of dominant landscapes. Petrophytic steppe vegetation consists of herbs with the participation of grasses and sedges and includes 62 vascular species. Yurtsev [55, 56] considers many of these species the most probable components of the former Pleistocene tundra-steppe (e.g. *Calamagrostis purpurascens* R. Br., *Carex pediformis* C.A. Mey, *Festuca kolymensis* Drobov, *Phlox sibirica* L., *Silene stenophylla* Ledeb., *Pedicularis venusta* Schang. ex Bunge, *Allium strictum* Schrad, etc.). The pebbly soils of the petrophytic steppe are characterised by a low moisture content, contrasting temperature regime and relatively high summer temperatures. They differ from the northern taiga soils by the presence of humus-accumulative horizons with abundant roots and a powdered structure; decreased actual and potential acidities; slightly higher exchangeable base contents, soluble salts, and organic nitrogen. The petrophytic steppe soils of the Kolyma Lowland have many features in common with the cryoarid soils of the more southern regions in Siberia [40], which are included in the modern Russian classification [26].

The biological activity showed that the microbocenoses of petrophytic steppe soils have some features which are typical of arid soils. Their profiles are characterised by a higher saturation of microorganisms and an active development of actinomycetes resistant to high insolation and moisture deficit. The microbial pools of different ecological-trophic groups in the petrophytic steppe soil exceed those in the soils of the adjacent sparse larch forests by one to two orders of magnitude. The steppe soils are also characterised by relatively high pools of the redox enzymes dehydrogenase and polyphenol oxidase participating in humus biogenesis; the biological destruction of plant residues and humification occur more actively in these soils.

The relic petrophytic steppe is characterised by high productivity. The growth rate of the aboveground phytomass (ANP) is comparable to the corresponding values of true steppes in Central Asia (China, Inner Mongolia, Transbaikalia, Khakasia) and significantly exceeds those of the modern arctic and subarctic tundras in America and Asia. Thus, our studies confirm the opinion of Yurtsev [55, 56] and Guthrie [2] that the productivity of Pleistocene high-latitude steppes was closer to that of modern temperate steppes than modern tundras and forest-tundras.

During the Last Glacial Maximum, the mammoth steppe was the largest biome on the Earth. It spread from western Europe to the east through all of Eurasia and Beringia to Canada, and from China in the south to the area of modern arctic islands in the north [2, 3, 55, 57-60]. The biome had a cryoarid climate, with a dry summer and a colder dry winter. Despite extensive long-term studies, the nature of the mammoth steppe is still not clear; however, its basis was undoubtedly composed of highly productive herbaceous ecosystems with tundra-steppe and steppe characteristics, which ensured a solid fodder base for large populations of large herbivorous mammals [2, 3, 58, 61].

Numerous palynological studies of mammoth fauna sites and the gastrointestinal contents of frozen mammoth fauna mammals carcasses were carried out in Northeast Siberia, including in the Kolyma Lowland [18, 19, 20, 22, 60-66]. Palynological data for the periods of the Zyryanian and Sartanian glaciations (MIS4, MIS2), as well as the cold phases of the Karginian (MIS3) interstadial, in the studied region confirm the wide development, up to dominance, of herbaceous, sedge-grass, and grass-wormwood associations with patches of moss cover. The various secondary taxons of plant communities, from humid biotopes to biotopes on dry stony slopes, indicate a wide range of habitats. Willow was a common shrub. Different authors have interpreted these landscapes as periglacial vegetation, herbaceous meadow-tundras with a dominance of grasses, grass and grass-wormwood tundra-steppes, cryoxerophilic herb communities, dry herbaceous tundra, cold steppes and arctic steppes. All these concepts largely reflect the dominance of open herbaceous (steppe, stepped, meadow) biotopes with patches of tundra vegetation and shrubs on plains and alpine tundras and steppes in mountainous regions, which creates a peculiar mosaic of biotopes favourable for the coexistence of different large phytophagous species [2, 56, 67]. The petrophytic steppe of the lower Kolyma reproduces one of the mosaic elements of the mammoth steppe.

The high productivity of herbaceous communities in the mammoth steppe is confirmed by the composition of the inhabiting mammals. Thus, remains of horses and steppe bisons (typical herbivorous species) are strongly dominant in the mammoth fauna sites of the Kolyma Lowland. Remains of woolly mammoth feeding on both grass and shrubs usually occupy the third or fourth position, the same as reindeer remains [18, 19, 68]. This fauna is known to also include other large herbivorous species (steppe species: saiga-antelope; arctic species: muskox; mountainous species inhabiting plains in the Late Pleistocene: Siberian snow sheep). Another species of the mammoth fauna, the woolly rhino, is of interest. This predominantly herbivorous species was obligate species in the mammoth steppe, but was usually not numerous [22, 69, 70]. In the Lower Kolyma River area, in the piedmonts region on the right bank, where we studied the relic petrophytic steppe, an unprecedentedly large amount of woolly rhino remains have been revealed; this is the richest location in terms of remains of this species. Tens of the woolly rhino horn fragments, several craniums and numerous skeleton fragments were found during gold mining on three fields (about only 20 m² in area) [21, 22]. Apparently, this herbivorous animal found here sufficient food on hills and watersheds. In our opinion, woolly rhinos were attracted by the steppe landscapes, some fragments of which still remain on the southern slopes of elevations. In 2007, a frozen mummy of a woolly rhino (which lived in the early Karginian interstadial, 43,324±592 cal yr BP) was found in the study region. It is noteworthy that the palynological analysis of deposits enclosing the carcass showed the dominance of pollen from the steppe and meadow-steppe plants, on which the animal apparently fed before its death [22].

At the boundary between the Pleistocene and Holocene, the cold steppes of Beringia began to be fragmented, having been degraded because of climate warming and wetting, and gradually substituted by tundra and taiga; this was the main factor for the extinction of the typical mammoth megafauna species.

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