



# Long-term ecology and conservation of the Kungur forest-steppe (pre-Urals, Russia): case study Spasskaya Gora

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## Abstract

The Kungur forest-steppe is the northernmost outpost of European forest-steppe, located in the western pre-Urals within the boreal climatic zone. The co-existence of boreal, nemoral and steppe species with relicts and endemics results in a high plant diversity, making it an important biodiversity hotspot. Under current climate change and strong agricultural impacts, the Kungur forest-steppe is rapidly degrading. In order to develop sustainable management strategies, we studied the vegetation history over the last 3500 years in the natural reserve area Spasskaya Gora. Palynological data indicate that the territory of Spasskaya Gora was largely covered by hemiboreal forests with high proportion of elm during the late Holocene. An opening of the vegetation strongly correlates with erosion, both indicating anthropogenic activities such as lumbering, agriculture, grazing and hay making. The modern *Pinus* and *Betula* dominated forests combined with large areas dominated by grasses and herbs appear in the last 300 years and caused by human activity. The data support the ‘anthropogenic’ hypothesis of the Kungur forest-steppe development, suggesting that Pleistocene steppe was replaced by hemiboreal forests during the Holocene. Steppe elements survived on exposed rocks. The recent forest-steppe landscapes dominated by pioneer birch and poplar were formed due to anthropogenic deforestation. With respect to nature conservation, our data demonstrate that prohibition of any anthropogenic activities at Spasskaya Gora will lead to loss of diversity of steppe assemblages over the mid-term. We emphasize that conservation of the high plant diversity of the Kungur forest-steppe must include disturbance factors in the form of selective lumbering, prescribed burning, moderate grazing or traditional mowing.

**Keywords** Boreal forest-steppe · Palynology · Vegetation history · Land-use history · Sustainable management · Biodiversity

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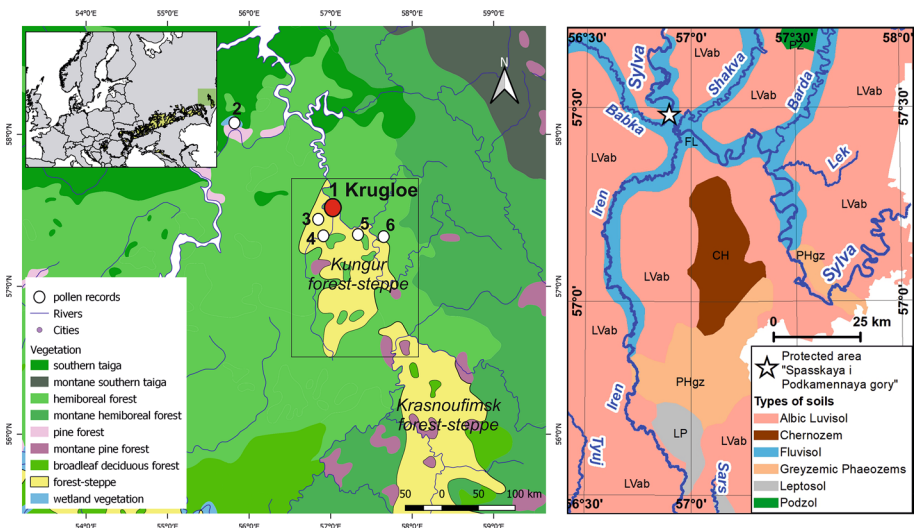
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## Introduction

The East European forest-steppe is a mosaic vegetation complex consisting of woody and herbaceous patches covering large areas from the Carpathians to the Ural Mountains (Fig. 1). Compared to other ecosystems in the region, it has relatively high net primary production, biomass and carbon sequestration capacity (Erdős et al. 2018a, 2019). Its fertile soils also make the zone important from an economic perspective in terms of potential gain from conversion to arable. Therefore, forest-steppe is among the most threatened ecosystems due to habitat loss, fragmentation and an inadequate network of protected areas. High species diversity, presence of relict populations of species that were once much more widespread and endemics make this zone of special conservation interest. Recent studies on European steppe outposts in Central Europe demonstrated that these extrazonal steppes harbour regionally endemic genetic lineages, large genetic diversity and a mosaic of stable refugia (Kirschner et al. 2020). Preservation of such habitats is crucial for conserving the biological diversity.

The Kungur forest-steppe is the northernmost outpost of the European forest-steppe located within the boreal climatic zone (Fig. 1). The highly heterogeneous geological, geomorphological and edaphic conditions on a rather small-scale allow the co-existence of boreal, nemoral and steppe species. This results in high plant diversity with 957 higher plant species, making the region an important biodiversity hot-spot in the boreal zone (Ovesnov 2009a). The special character of the Kungur forest-steppe is shown by its typical forest-steppe plant assemblages. The woodlands are dominated by *Betula pendula*, *Populus tremula* and *Pinus sylvestris* forests associated with *Tilia cordata* and *Ulmus glabra*. Typical forest-steppe shrubs such as *Cerasus fruticosa*, *Chamaecytisus ruthenicus*, *Rhamnus cathartica*, *Cotoneaster melanocarpus* and *Genista tinctoria* grow



**Fig. 1** Vegetation map (left; based on Bohn et al. 2003) with the location of the Kungur forest-steppe and pollen records: (1) Krugloe (this study), (2) Chernaya (Shumilovskikh et al. 2020a, b), (3) Kriukovy and (4) Dubovoe (Genkel 1957), (5) Ust-Kishert (Golubeva 1956), (6) Osintsevo-1 (Elovicheva 1991). Soil map (right; based on Signaevskiy 1989) with location of the protected landscape “Spasskaya i Podkamennaya Gory”

in the understory. The steppe vegetation includes petrophytic steppes on carbonate and gypsum outcrops as well as meadow steppes and shrub-meadow steppes on watershed areas and ‘floodplain’ steppes (Ponomarev 1940, 1948, 1949; Ovesnov 2009b).

Due to its fertile soils, the region is intensively used for agriculture. As a result, 40–50% of the area is covered by arable land and only 10–20% by semi-natural vegetation (Ovesnov 2009b). Most remaining areas of steppe ecosystem are situated on unsuitable for cropping positions such as steep slopes, deep ravines and karstic fields. Today, the most widespread factors of steppe degradation are overgrazing, uncontrolled recreation, timber exploitation, forest plantations and mining. Furthermore, an increase of precipitation in the Perm region in recent years (Abdullin and Shikhov 2019; Shaumova et al. 2010; Shikhov et al. 2020) might cause the replacement of steppe species by meadow and forest species. Sannikov et al. (2014a, b) demonstrated that the Kungur forest-steppe, and especially its steppe assemblages, is degrading, and strongly recommended increasing the area under nature protection. An understanding of the vegetation history is generally necessary to develop sustainable management strategies for biodiversity conservation (e.g. Whitlock et al. 2017) and this is especially true for the Kungur forest-steppe.

The Holocene dynamic of the Kungur forest-steppe is poorly studied. The proposed ideas can be grouped in two major concepts. The ‘anthropogenic’ concept suggests that Pleistocene steppe was replaced by hemiboreal forests during the Holocene, while steppe elements survived only along rivers and on exposed rocks. Due to anthropogenic deforestation, steppe elements spread and form the recent forest-steppe landscapes with dominance of pioneer taxa such as *Betula* (Korzhinsky 1887; Krasovskiy and Sergeeva 1933). The ‘Pleistocene relict’ concept proposes that Siberian birch forest-steppe dominated the landscapes during the entire Holocene until today (Korzhinsky 1891; Krasheninnikov 1939; Ovesnov 2009b; Ponomarev 1948). Although few pollen records exist (Genkel 1957; Golubeva 1956; Elovicheva 1991), the lack of well-dated archives hampers the examination of these concepts.

In order to close this gap, we carried out a palaeoecological study at the Spasskaya Gora, a protected area located at the northern border of the Kungur forest-steppe. Based on palynological, radiometric and sedimentological investigations on the sediment core from the Lake Krugloe, we present the vegetation history of the Spasskaya Gora, evaluate concepts of the origin and development of the Kungur forest-steppe and suggest management strategies for nature protection in the region.

## Relict forest-steppe flora and concepts on origin and development of the Kungur forest-steppe

The very special floristic character of the Kungur forest-steppe within the vegetation of the pre-Urals was highlighted already at the end of the ninth–beginning of twentieth century (Korzhinsky 1887, 1891; Krylov 1878; Siuzev 1912). The Kungur forest-steppe is known as a unique natural phenomenon bearing endemics and relicts of different ages (Gorchakovskiy 1967, 1969; Krasheninnikov 1939; Ovesnov 2009b; Ponomarev 1948).

Within the protected landscape “Spasskaya i Podkamennaya Gory”, six endemic plant species were recorded (Kulikov et al. 2013). *Agropyron reflexiaristatum* (*Elytrigia reflexiaristata*) is a petrophilous endemic of the Urals distributed from the southern part of the Urals to the southern part of the Northern Urals. *Anemone uralensis* is a Ural endemic nemoral species. *Libanotis krylovii* (*Seseli krylovii*) is a subboreal-montane endemic

of the Urals distributed from the Southern to the Northern Urals. *Thymus hirticaulis* is a petrophilous endemic of the Urals and Pre-Urals (distributed from the Northern to the Polar Urals). *Euphorbia korshinskyi* is a subendemic of the Urals and Pre-Urals. *Oxytropis kungurensis* (*O. uralensis*) is a mountain-steppe endemic of the Middle Urals within the Kungur and Krasnoufimsk forest-steppe. These Ural mountain-steppe and petrophilous endemics are considered as peculiar relicts of the Tertiary stony steppe flora (Gorchakovsky 1969) or of the Pleistocene glacials (Kulikov et al. 2013).

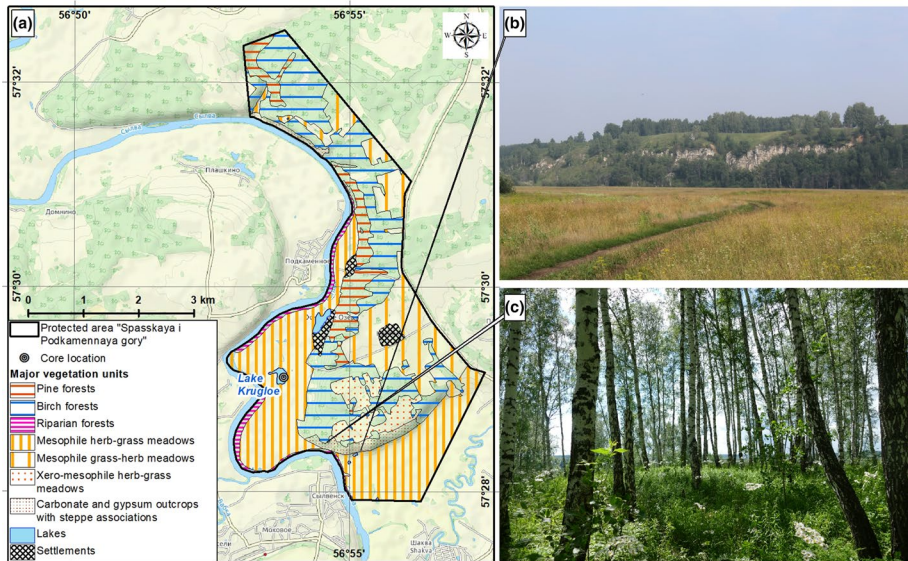
According to Gorchakovsky (1969), relict plant species of the Kungur forest-steppe can be divided into three main groups. The first group of Pliocene relics found at Spasskaya Gora includes *Laser trilobum*, *Geranium robertianum* and *Digitalis grandiflora*, growing mainly in the elm-birch-lime forests. In general, in the Urals, *Laser trilobum* and *Digitalis grandiflora* mainly occur in open pine and birch forests, or in pine–birch associations. The main habitat of *Geranium robertianum* is in deciduous forests and in dark coniferous forests with an admixture of linden. It is suggested that linden-spruce-fir forests were much more widespread during the Pliocene. In the Pleistocene, general cooling and repeated glacial periods led to the spread of dark coniferous forests dominated by spruce and fir and an almost complete loss of broad-leaved elements.

The second group of petrophilous and mountain-steppe species *Agropyron reflexiaristatum*, *Oxytropis kungurensis* and *Alyssum obovatum* as well as forest species such as *Anemone uralensis*, *Saussurea controversa* and *Geranium pseudosibiricum* are considered as Pleistocene relicts. In addition to endemics *Oxytropis kungurensis* and *Agropyron reflexiaristatum*, *Alyssum obovatum* is a cryoxerophytic species suggested to be a Pleistocene periglacial steppe relict of South Siberian origin. The origin of the relict steppe petrophytic communities is associated with the vegetation of the cold and dry phases of the Pleistocene (Kulikov et al. 2013; Ponomarev 1948).

The last group is the most abundant in the protected area and determines the special character of steppe meadows and stony steppes of the Kungur forest-steppe. It includes warm steppe species such as *Stipa pennata*, *Artemisia frigida*, *Artemisia latifolia*, *Echinops ritro*, *Filipendula hexapetala*, *Onosma simplicissima*, *Helictotrichon desertorum*, *Gypsophila altissima*, *Oxytropis pilosa*, *Spiraea crenata*, *Aster alpinus*, *Artemisia sericea* and *Anemone sylvestris*. These species are considered as relicts of the Holocene thermal maximum (Ponomarev 1948).

The Tertiary and Pleistocene vegetation history of the western pre-Urals has been described by Gorchakovskiy (1967, 1969), Krasheninnikov (1939) and Ponomarev (1948). At the end of the Tertiary (2.6 million years ago), general climate cooling induced the replacement of the broad-leaved forests by boreal forests. During the glacial periods of the Pleistocene (2.6 million–11,700 years ago), *Larix-Pinus-Betula* forest-steppe dominated the landscapes. During harsh cold conditions, broadleaved forest remains survived in the Southern Urals, as indicated by presence of several nemoral endemic species. During interglacial periods, nemoral species spread from their glacial refugia, while dark conifers such as spruce and fir spread from Siberia and the Altai Mountains.

Two major competing concepts have been developed to describe the Holocene (11,700 years ago-present) history of the Kungur forest-steppe. The ‘anthropogenic’ concept suggests a leading human role in establishment of the modern forest-steppe (Korzhin-skiy 1887; Krasovskiy and Sergeeva 1933). They argued that the Pleistocene steppe was replaced by hemiboreal forests during the Holocene and steppe elements could survive along rivers and on exposed rocks. Land use and deforestation led to the establishment of secondary birch and pine forests and spread of steppe elements in upland areas. The ‘Pleistocene relict’ concept suggests that the Siberian type Pleistocene birch forest-steppe



**Fig. 2** Study site: **a** map of the natural reserve “Spasskaya i Podkamennaya Gory” with major vegetation units; **b** view of gypsum outcrops with the petrophytic steppe and birch open forests (Photo P. Sannikov); **c** typical birch forest patch (Photo L. Shumilovskikh)

dominated the landscapes of the Kungur forest-steppe during the entire Holocene (Korzhiński 1891). This concept has a few variations. Krasheninnikov (1939) proposed the dominance of the Pleistocene pine-larch-birch cold forest-steppe during the late glacial, migration of warm forest-steppe elements during the xerothermic period of the Holocene and final spread of spruce and formation of hemiboreal forests with steppe slopes to the present. Applying this hypothesis to the Kungur forest-steppe, Ponomarev (1948) proposed two migration waves: (1) late Pleistocene/early Holocene migration of eastern Siberian steppe elements, and (2) late Holocene xerothermic invasion of the European steppe species. However, he did not comment on the general vegetation changes during the Holocene. Gorchakovskiy (1967) suggests that the Kungur, Krasnoufimsk and Mesiagutovsk forest-steppe regions were all part of one single large steppe and forest-steppe area in the middle Holocene, which developed into the modern birch-pine forest-steppe in the late Holocene. The followers of this concept highlight the negative anthropogenic impact, whereby land use led to a strong decline of forest-steppe areas and their fragmentation.

## Regional setting

### Geographical setting

The protected area Spasskaya Gora is a part of the protected landscape “Spasskaya i Podkamennaya Gory” (Perm region, Russia) with a total area of 950 ha. It is located on the eastern part of the East-European Plain, in the Sylva-Iren lowland, occupying the right bank of the Sylva River valley and part of the upland area (Fig. 2). The flood plain is

situated at altitudes from 110 to 113–114 m above sea level (a.s.l.). Terraces up to 1.5 km width and up to 6–7 m high are present in the southern and central parts. Gypsum rock exposures with partly very steep slopes occur in the northern and southern parts reaching up to 150–160 m a.s.l. (Fig. 2). Slightly sloping or flat uplands reach up to 190–200 m a.s.l. Karst processes represented by numerous sink holes, lakes, ponors, and caves play a significant role in landscape development (Kadebskaja 2009).

The climate of the Perm region is continental with long cold and snowy winters and warm short summers. The average annual temperature in Kungur is 1.8 °C (– 15.3 °C in January, 18.1 °C in July). The annual precipitation is 517 mm (16–19 mm in February–March, 81 mm in July). Snow and ice cover last for 6 months between October–November and April–May (Tartakovskiy 2012; Shklyayev and Shklyayeva 2006).

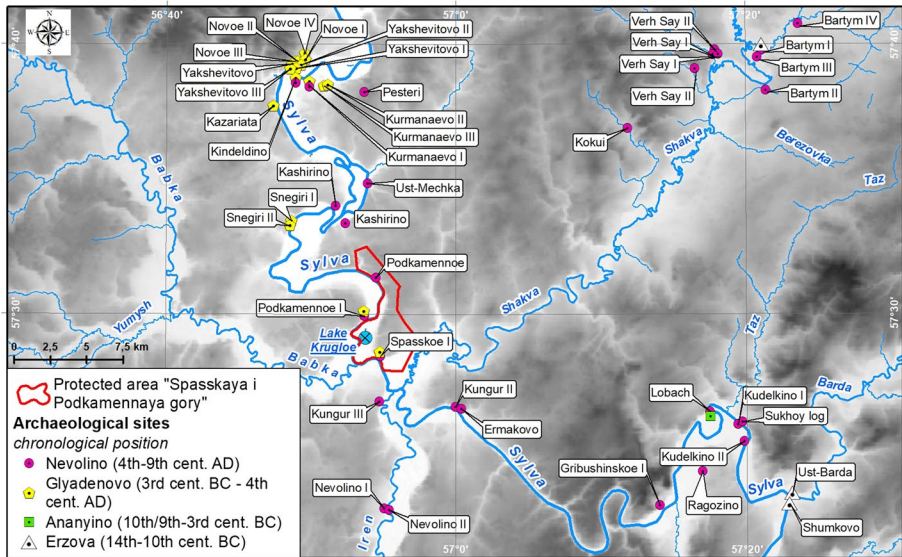
Geologically, the Kungur forest-steppe is located on the eastern end of the Russian plate, in the western part of pre-Urals. The underlying geology is formed by Paleozoic sediments belonging Irenskaya Suite of the Kungurian Stage of the Lower Permian. These are dolomites, dolomitic limestones with layers of anhydrites, chalky clays and carbonate breccia. The basement rock reaches 4–5 km deep (Kadebskaja 2009; Tartakovskiy 2012).

The Kungur forest-steppe is characterised by the dominance of dark-coloured soils that differ from the podzol soils of neighbouring regions (Eremchenko et al. 2010; Korotaev 1962; Fig. 1). The protected landscape “Spasskaya i Podkamennaya Gory” belongs to the Kama province of the zone of grey-forest soils (Shoba 2011) or Greyzemic Phaeozems according to the World Reference Base for Soil Resources (IUSS Working Group WRB 2015). The heterogeneous geological and relief structure of the protected landscape caused the formation of diverse soils. Grey and dark-grey soils (Greyzemic Phaeozems) on upland are fertile and were ploughed in former times, leading to the formation of Phaeozems (Anthric) and Anthrosols. Typical for southern taiga Albic Luvisols occur on slope, while Calcaric/Gypseric Rendzic/Mollic Leptosols on carbonates and gypsum on steep slopes. Depending on the steepness of slopes, soil profiles vary from a few centimetres to 1.5 m. Sandy soils (Arenosols) with a thin humus horizon of 1.5–5 cm can be found in ravines and their slopes. On the terraces, meadow soils with a thick humus layer up to 35 cm (Cambic/Chernic Phaeozems) are widespread and were ploughed forming Anthrosols. Alluvial, poorly differentiated soils (Fluvisols) are formed close to the river.

## Vegetation

The flora of “Spasskaya Gora” contains 451 species of vascular plants belonging to 274 genera and 73 families (Ovesnov and Efimik 2014, Supplementary Table). Forests cover about 44% of the area, mainly consisting of *Pinus sylvestris*, *Betula pendula*, *Populus tremula*, *Ulmus laevis*, *Tilia cordata*, *Picea obovata*. Open vegetation is mostly steppe-meadows on the upland (28%), alluvial meadows on the terraces (21%) and petrophytic steppe on steep slopes (4%) (Fig. 3b). The coexistence of forest, meadow and forest-steppe species is determined by the steepness and exposure of slopes and edaphic conditions.

Pine forests and open birch forests (in Russian: ‘kolki’; Fig. 2c) are located on the slopes and on upland areas of Spasskaya Gora. Forests located on upland areas are apparently secondary. Their shrub layer contains a large number of forest and meadow species, while steppe elements are rare (Table 1). Most of these forests have been cleared for timber, agricultural use, haymaking or pasture. Spruce–birch forests are located on the lower parts of the slopes. Linden–birch–aspen forests (*Tilia cordata*, *Betula pendula*, *Populus tremula*) are found in depressions on the uplands with herb layer indicating humid conditions



**Fig. 3** Overview of archaeological sites around the study region

(Table 1). Elm–birch–linden (*Ulmus laevis*–*Betula pendula*–*Tilia cordata*) forests occupy small areas in the lower part of the slope, closer to the river floodplain and oxbow lakes. Steppe-like meadows and meadow steppes are present in the uplands and on its slopes and include a large number of steppe and forest-steppe species (Table 1). Rich in relict and endemic species petrophytic *Artemisia*-steppe associations are developed on steep southern slopes (Fig. 2b; Table 1). Almost the entire upland area and meadows on the terraces were ploughed in the past or used for hayfields. Mesophilic meadows are dominated by meadow and weedy/ruderal species, sometimes with the inclusion of steppe and forest-steppe species (Table 1). The abandoned upland meadows are currently overgrown mainly with *P. sylvestris*.

Lake Krugloe is located in the alluvial plain of the Sylva River (Fig. 2a), experiencing seasonal flooding after snow melting in April. The size of the lake is approximately 300×300 m. It is surrounded by a belt of *Ulmus laevis* with *Salix* and *Rubus caesius* and mesophilic meadows..

## Archaeology and settlement history

The colonisation of the Sylva River area began in the Late Bronze Age with the Erzova culture (fourteenth–tenth century BC) found at Shumkovo, Ust-Barda, Ust-Gromotukha and Shatovo (Fig. 3). The Late Bronze Age culture transformed to Early Iron Age Ananyino culture (tenth/ninth–third centuries BC), continuing their traditions (Fig. 3). The economic basis of the Bronze Age populations in the Kama region was a mixed form of household with a gradually increasing role of animal husbandry mainly by cattle and horses (Petrenko 2007). Livestock breeding, especially of horses, increased in the Ananyino culture (Koreniuk et al. 2018). Analysis of animal bone remains shows the dominance of 1- and 2-year

**Table 1** Description of major vegetation taps of the natural reserve Spasskaya Gora

Vegetation type	Geomorphology	Dominant taxa
Semi-natural pine forests	Steep slopes	Trees: <i>Pinus sylvestris</i> Shrubs: <i>Cerasus fruticosa</i> , <i>Chamaecytisus ruthenicus</i> , <i>Cotoneaster mel-anocarpus</i> , <i>Genista tinctoria</i> , <i>Juniperus communis</i> Herbs: <i>Artemisia sericea</i> , <i>Calamagrostis arundinacea</i> , <i>Carex pediformis</i> , <i>Dendranthema zawadskii</i> , <i>Dracocephalum ruyschiana</i> , <i>Galium boreale</i> , <i>Helianthemum nummularium</i> , <i>Helictotrichon desertorum</i> , <i>Onosma simplicissima</i> , <i>Phleum phleoides</i> , <i>Pteridium aquilinum</i> , <i>Rubus saxatilis</i> , <i>Salvia stepposa</i> , <i>Solidago virgaurea</i> , <i>Stipa pennata</i> , <i>Trifolium montanum</i> , <i>Veronica spicata</i> , <i>Viola collina</i>
Open birch forests	Upper part of the slopes and on the upland areas	Trees: <i>Betula pendula</i> Shrubs: <i>Genista tinctoria</i> Herbs: <i>Artemisia macrantha</i> , <i>Artemisia sericea</i> , <i>Brachypodium pinnatum</i> , <i>Calamagrostis epigeios</i> , <i>Galium boreale</i> , <i>Inula hirta</i> , <i>Lathyrus vernus</i> , <i>Libanotis montana</i> , <i>Origanum vulgare</i> , <i>Phleum phleoides</i> , <i>Pulmonaria mollis</i> , <i>Pyrethrum corymbosum</i> , <i>Trifolium medium</i> Trees: <i>Betula pendula</i> , <i>Picea obovata</i> Herbs: <i>Limnace borealis</i> , <i>Maianthemum bifolium</i> , <i>Orthilia secunda</i> , <i>Oxalis acetosella</i>
Spruce–birch forests	Lower part of the slopes	
Linden–birch–aspen forests	Depressions on upland	Trees: <i>Betula pendula</i> , <i>Populus tremula</i> , <i>Tilia cordata</i> Herbs: <i>Aconitum septentrionale</i> , <i>Aegopodium podagraria</i> , <i>Alchemilla vulgaris</i> , <i>Cirsium heterophyllum</i> , <i>Dactylis glomerata</i> , <i>Deschampsia cespitosa</i> , <i>Geranium sylvaticum</i> , <i>Milium effusum</i> , <i>Polygonum bistorta</i> , <i>Sanguisorba officinalis</i>
Elm–birch–linden forests	Lower part of the slope close to the river flood-plain and oxbow lakes	Trees: <i>Betula pendula</i> , <i>Tilia cordata</i> , <i>Ulmus laevis</i> Shrubs: <i>Rhamnus cathartica</i> , <i>Rubus caesius</i> Herbs: <i>Aegopodium podagraria</i> , <i>Asarum europaeum</i> , <i>Inula salicina</i> , <i>Polygonum odoratum</i> , <i>Pteridium aquilinum</i> , <i>Origanum vulgare</i> , <i>Digitalis grandiflora</i> , <i>Laser trilobum</i> , <i>Cephalanthera rubra</i> , <i>Libanotis montana</i> , <i>Pyrethrum corymbosum</i> , <i>Viola collina</i>



**Table 1** (continued)

Vegetation type	Geomorphology	Dominant taxa
Steppe-like meadows and meadow steppes	Upland, slopes	Herbs: <i>Adonis vernalis</i> , <i>Agrimonia eupatorioides</i> , <i>Anemone sylvestris</i> , <i>Artemisia macrantha</i> , <i>Artemisia sericea</i> , <i>Aster amellus</i> , <i>Astragalus damicus</i> , <i>Calamagrostis epigeios</i> , <i>Campanula bononiensis</i> , <i>Filipendula vulgaris</i> , <i>Fragaria viridis</i> , <i>Inula hirta</i> , <i>Inula salicina</i> , <i>Libanotis montana</i> , <i>Onobrychis arenaria</i> , <i>Origanum vulgare</i> , <i>Phlomis tuberosa</i> , <i>Pyrethrum corymbosum</i> , <i>Stipa pennata</i> , <i>Trifolium medium</i> , <i>Vicia tenuifolia</i>
Petrophytic <i>Artemisia</i> -steppe	Steep southern slopes	Herbs: <i>Agropyron reflexiaristatum</i> , <i>Allium strictum</i> , <i>Alyssum obovatum</i> , <i>Artemisia frigida</i> , <i>Artemisia macrantha</i> , <i>Artemisia sericea</i> , <i>Aster alpinus</i> , <i>Astragalus cornutus</i> , <i>Campanula sibirica</i> , <i>Echinops ritro</i> , <i>Festuca rupicola</i> , <i>Filipendula vulgaris</i> , <i>Gypsophila altissima</i> , <i>Helianthemum nummularium</i> , <i>Onosma simplicissima</i> , <i>Oxytropis pilosa</i> , <i>Polygala sibirica</i> , <i>Potentilla humifusa</i> , <i>Sabia stepposa</i>
Mesophile grass-herb and herb-grass meadows	Terraces and upland	Herbs: <i>Achillea millefolium</i> , <i>Aegopodium podagraria</i> , <i>Arrhenatherum elatius</i> , <i>Artemisia vulgaris</i> , <i>Bromus inermis</i> , <i>Centaurea scabiosa</i> , <i>Cirsium arvense</i> , <i>Dactylis glomerata</i> , <i>Equisetum arvense</i> , <i>Festuca pratensis</i> , <i>Fragaria viridis</i> , <i>Galium mollugo</i> , <i>Hieracium sosnowskyi</i> , <i>Leucanthemum vulgare</i> , <i>Medicago sativa</i> , <i>Melilotus albus</i> , <i>Phleum pratense</i> , <i>Picris hieracioides</i> , <i>Pimpinella saxifraga</i> , <i>Plantago media</i> , <i>Poa pratensis</i> , <i>Potentilla anserina</i> , <i>Prunella vulgaris</i> , <i>Pyrethrum corymbosum</i> , <i>Ranunculus acris</i> , <i>Ranunculus polyanthemos</i> , <i>Rumex crispus</i> , <i>Sonchus arvensis</i> , <i>Taraxacum officinale</i> , <i>Trifolium montanum</i> , <i>Trifolium medium</i> , <i>Veronica teucrium</i> , <i>Vicia cracca</i> , <i>Vicia sepium</i>

old animals, indicating the purpose of animal husbandry as food production (Petrenko 2007).

The archaeological sites of the Glyadenovo culture (third century BC–sixth century AD) are more numerous (Fig. 3). The sites are located in groups with areas of 5–10 km radius around each group. Analyses of archaeological sites and ceramics indicate a slow colonization of the Sylva river banks by the Glyadenovo population, reaching the mouth of the Shakva River towards the end of the fourth century AD. The economy of the Glyadenovo period was also based on domestic animal breeding, indicated by dominance of domestic livestock bones (up to 94–100%) in the waste of the settlements (Koreniuk et al. 2018). Most possibly floodplain meadows were used for grazing and haymaking (Pereskokov 2018). Rare findings indicate the development of agriculture with emmer and barley (Poliakov 2001).

Numerous medieval archaeological sites of the Nevolino culture (end of the fourth–ninth centuries AD) are located in the Sylva River area, mainly along its two tributaries the Shakva River and the Iren River (Fig. 3). The relevance of domestic animals in the medieval diet is markedly reduced in comparison with the Glyadenovo period (Goldina et al. 2012). A significant number of fishing hooks, harpoons and “kibases” indicate highly developed fishing techniques (Goldina et al. 2012). A strong development of agriculture is indicated by agricultural tools as well as pits filled with grains of wheat, emmer, rye, oats and barley in the archaeological sites of the seventh–ninth centuries Verkh-Saya I, Lobach and Bartym I (Goldina et al. 2012).

## Methods

### Sediment core and age-depth model

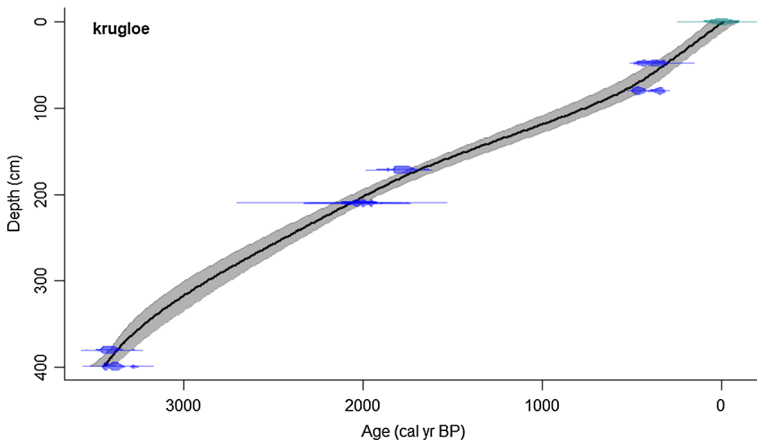
The coring of Lake Krugloe was carried out from ice in March 2018 using a Russian corer. Two overlapping cores were obtained at a distance of one meter from each other. The core Krugloe I (2) (57°29′07.5″N 56°53′48.4″E 109 m a.s.l.; 400 cm long) is used in this study. The depth from the ice surface to the top of the core was 160 cm. The obtained sediments were described in the field. The core sections were packed in plastic, transported to the laboratory in Göttingen (Germany) and kept in a cold room at 4 °C.

To determine the organic, carbonate and mineral contents of the core, 200 samples of 1 cm<sup>3</sup> volume were taken at intervals of 2 cm for loss-on-ignition (LOI) analysis following a standard protocol (Heiri et al. 2001). The values were calculated as a percentage of the sediment dry weight.

Seven samples (Table 2) were dated by the AMS radiocarbon method in the Radiocarbon Laboratory of Poznań (Poland). The data were calibrated using IntCal20 (Reimer et al. 2020) and used for establishment of the age-depth model (Fig. 4) with the clam 2.2 package (Blaauw 2010) in R (R Core Team 2020). The smooth spline was used with a smoothing level of 0.4.

### Palynology

For laboratory analysis, 1 cm<sup>3</sup> of material was taken with intervals 8–20 cm. One tablet of *Lycopodium* spores (batch number 1031) was added to each sample to enable calculation



**Fig. 4** Age-depth model of the sediment core Krugloe

of pollen concentration (Erdtmann 1960). Samples were processed by treating with 10% HCl, sieving through a metal sieve at 200  $\mu\text{m}$ , cold 48% HF for one night, then sieving through a nylon sieve at 5  $\mu\text{m}$ . Acetolysis was not used in order to preserve algal remains (Shumilovskikh et al. 2019). The remaining pellet was stored in glycerin and studied under 400 $\times$  magnification. Pollen identification and taxonomy follows Beug (2004). Non-pollen palynomorphs were identified using Non-Pollen Palynomorph Image Database (Shumilovskikh et al. 2021). Microcharcoal particles > 50  $\mu\text{m}$  were counted in order to estimate fire activities (Clark 1988). The pollen sum of minimum 300 terrestrial pollen grains (average 370) was used for calculation of pollen and NPP percentages (Fig 5). The pollen diagram was created using C2 (Juggins 2007).

In order to identify reliable pollen indicators for forest-steppe vegetation, plant species known in Spasskaya Gora were related to pollen taxa following Beug (2004) (Table 3; Supplementary Table). The geographical distribution of plant species is based on Ovesnov et al. (2007) and Naumenko (2008).

## Results

### Sedimentology and age-depth model

The entire core is characterised by greyish green minerogenic silt with visible fine plant remains. LOI show very high percentage of inorganic material varying between 85 and 98%. Phases of an increased inorganic content occur at 384–294 (89–91%), 204–124 cm (88–90%), 20–6 cm (88–89%). The carbonate content of about 2% stays until 78 cm (~1455 years BP), rising after this depth to 4% and show several peaks up to 12% (Fig. 5).

We used bulk, terrestrial plant remains and wood for radiocarbon dating of the sediment core (Table 2). The direct comparison of the dates for plant remains and bulk from a depth of 210 cm revealed that the bulk sample is about 810 years older than the plant sample, most possibly due to the hard water effect. For construction of the age-depth model,

**Table 2** List of radiocarbon samples from the core Krugloe

Core depth	Laboratory ID	Material	C14	Remarks	Calendar age, year BP (probability)
48–50 cm	Poz-125579	2 <i>Filipendula ulmaria</i> seeds, charred Poaceae and moss stems, charred leaf fragments, wood charcoal	335 ± 30 BP	0.18 mgC	313–472 (95%)
80 cm	Poz-111284	Bulk	1185 ± 30 BP		*318–392 (39.4%) 425–500 (55.6%)
171.5 cm	Poz-122531	cf. <i>Ulmus</i> wood with bark	1875 ± 30 BP		1714–1835 (91.5%) 1855–1866 (3.4%)
210 cm	Poz-119212	Bulk	2870 ± 30 BP		*1934–1934 (0.2%) 1936–2109 (94.6%)
210 cm	Poz-115861	<i>Populus</i> bud scale, Poaceae stem, <i>Bidens</i> seed fragment	2060 ± 110 BP	0.04 mgC	1747–1765 (1.4%) 1782–2312 (93.6%)
380 cm	Poz-107862	Bulk	4010 ± 35 BP		*3364–3467 (94%) 3475–3478 (0.9%)
399 cm	Poz-125580	<i>Populus</i> bud scale, Poaceae charred stem, <i>Filipendula ulmaria</i> seed, <i>Lythrum salicaria</i> seed, charred leaves, charred Poaceae stems	3160 ± 35 BP	0.16 mgC	3267–3287 (5.7%) 3335–3452 (89.1%)

Reservoir age of 810 years was applied for all bulk samples (noted by star in calendar age)

**Table 3** List of pollen taxa (after Beug 2004) including forest-steppe species in relation to the type of plant distribution

Plant distribution	Pollen taxa
Boreal–nemoral–forest-steppe	<i>Allium ursinum</i> -type, <u><i>Androsace alpina</i></u> -type, Apiaceae p.p., <i>Astragalus</i> -type, <i>Ballota</i> -type, Brassicaceae, Chenopodiaceae, <i>Lappula</i> , <i>Matricaria</i> -type, <i>Melampyrum</i> , <i>Mentha</i> -type, <i>Odontites</i> -type, Poaceae, <u><i>Polygonum alpinum</i></u> , <i>Potentilla</i> -type, <i>Ranunculus acris</i> -type, <i>Rhamnus</i> -type, <i>Rosa</i> , Rubiaceae, <i>Sanguisorba officinalis</i> , <i>Sedum</i> -type, <i>Senecio</i> -type, <i>Silene</i> -type, <i>Thalictrum</i> , <i>Trifolium pratense</i> -type, <i>Verbascum</i> , <i>Vicia</i> -type
Forest-steppe	<u><i>Adonis vernalis</i></u> , <i>Allium ursinum</i> -type, Apiaceae p.p., <i>Artemisia</i> , <i>Aruncus</i> -type, <u><i>Asparagus officinalis</i></u> -type, <i>Astragalus</i> -type, Brassicaceae, <i>Campanula trachelium</i> -type, Cichorioideae, <u><i>Cynoglossum</i></u> , Cyperaceae, <u><i>Cytisus</i></u> -type, <i>Dianthus</i> , <i>Euphorbia</i> , <i>Filipendula</i> , <i>Galeopsis</i> -type, <u><i>Genista</i></u> -type, <u><i>Gypsophila repens</i></u> -type, <u><i>Helianthemum nummularium</i></u> -type, <i>Hypericum perforatum</i> -type, <i>Lathyrus</i> -type, <u><i>Lithospermum officinale</i></u> -type, <i>Lotus</i> -type, <i>Matricaria</i> -type, <i>Mentha</i> -type, <i>Nonea pulla</i> , <i>Onobrychis</i> , <i>Orobanche</i> , <i>Phyteuma</i> -type, <i>Plantago major-media</i> -type, Poaceae, <i>Polygala comosa</i> -type, <i>Populus</i> , <i>Prunella</i> -type, <i>Ranunculus acris</i> -type, Rubiaceae, <i>Salvia pratensis</i> group, <i>Saussurea</i> -type, <i>Senecio</i> -type, <i>Sorbus</i> group, <u><i>Thesium</i></u> , <i>Trifolium</i> p.p., <i>Trifolium repens</i> -type, <i>Veronica</i> -type, <i>Viola</i>
Steppe	Brassicaceae, <u><i>Echinops</i></u> , <u><i>Onosma</i></u> , Poaceae, <i>Silene</i> -type

Underlined are taxa containing exclusively species with forest-steppe distribution (Supplementary Table)

the reservoir effect of 810 years was applied for all bulk samples. Based on the age-depth model (Fig. 4), the accumulation rate is 0.1–0.17 cm/year throughout the core.

### Relation of forest-steppe plant species and pollen taxa

The analysis of plant species growing today at Spasskaya Gora reveals 451 species of vascular plants, which are related to 174 pollen types (Supplementary Table). About 25% (110 species) of all species have a steppe or forest-steppe distribution, corresponding to 66 pollen taxa (Table 2). Six pollen taxa are related to boreal–nemoral–forest-steppe vegetation: *Androsace alpina*-type, *Lappula*, *Odontites*-type, *Polygonum alpinum*, *Rosa* and *Sanguisorba officinalis*. For the forest-steppe zone there are 14 indicative pollen taxa: *Adonis vernalis*, *Asparagus officinalis*-type, *Cynoglossum*, *Cytisus*-type, *Genista*-type, *Gypsophila repens*-type, *Helianthemum nummularium*-type, *Lithospermum officinale*-type, *Lotus*-type, *Nonea pulla*, *Onobrychis*, *Orobanche*, *Salvia pratensis* and *Thesium*. Only two taxa, *Echinops* and *Onosma*, are indicative for steppe.

Several pollen taxa include a few forest-steppe and non-forest-steppe species. For example, *Thalictrum* has one boreal–nemoral–forest-steppe species *Thalictrum minus* and one boreal species *T. simplex*. *Artemisia* includes five forest-steppe species: *A. commutata*, *A. frigida*, *A. latifolia*, *A. macrantha* and *A. sericea*. *Filipendula* includes the boreal *F. ulmaria* and forest-steppe *F. vulgaris*. *Saussurea*-type includes two forest-steppe species,

*Carlina biebersteinii* and *Serratula coronata*. *Trifolium repens*-type has one forest-steppe species, *T. lupinaster*, and two boreal species: *T. hybridum* and *T. repens*. These pollen taxa can be used for interpretation with caution. All other pollen types include numerous species with variable distribution.

## Pollen record and environmental changes

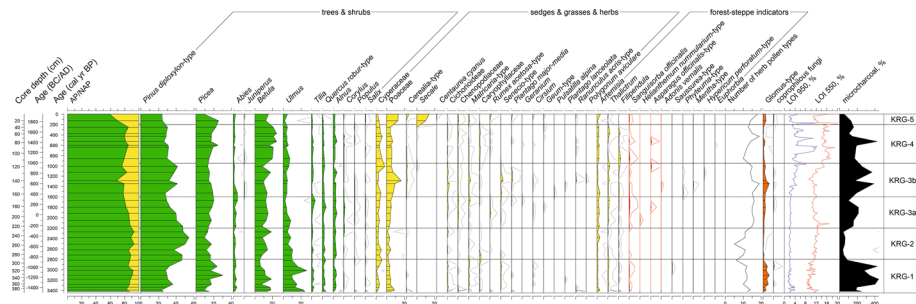
Pollen records from Krugloe reveal 82 pollen taxa, 27 of which contain forest-steppe species. The diagram is visually divided into 5 local pollen zones (LPZ; Fig. 5).

LPZ-1 (400–300 cm, 3500–2800 years BP) is characterized by the dominance of *Pinus diploxylon*-type (23–32%), *Ulmus* (9–26%), *Picea* (9–30%) and *Betula* (6–19%). Poaceae (4–9%) is accompanied by *Artemisia*, Cichorioideae, *Thalictrum*, *Matricaria*-type, *Senecio*-type, *Plantago major-media*, *Cirsium*, *Sanguisorba officinalis*. The occurrence of coprophilous fungi, a large amount of microcharcoal, increased *Glomus*-type and enhanced minerogenic content are representative for this zone.

In the LPZ-2 (300–225 cm, 2800–2200 years BP), the percentages of *Pinus* increase up to 37–54%, while values of *Picea* (9–18%) and *Ulmus* (5–10%) decrease. Poaceae decrease to 1–5% and the number of herb taxa decrease. Microcharcoals and *Glomus*-type decline, while organic content increases.

A strong change in pollen assemblages occurs in the LPZ-3 (225–115 cm, 2200–950 years BP). Poaceae reaches a maximum of 16%, *Pinus* (28–47%) and *Ulmus* (2–8%) decrease. Percentages of microcharcoals, *Glomus*-type and minerogenic content in the sediment increase again. In the LPZ-3a (225–165 cm, 2200–1600 years BP), the forest-steppe element *Sanguisorba officinalis* increases, *Asparagus officinalis*-type and *Helianthemum nummularium*-type occurs. The diversity of herbaceous pollen increases with *Senecio*-type, *Cirsium* and Chenopodiaceae. In the LPZ-3b (165–115 cm, 1600–950 years BP), Poaceae reaches a maximum and Cerealia-type increases. Among the herbs, *Adonis vernalis*, *Hypericum-perforatum*-type, *Matricaria*-type, *Senecio*-type, *Plantago major-media* increase and *Pulsatilla alpina* occurs.

LPZ-4 (30–115 cm, 1000–200 years BP) reveals an increase in *Betula* (16–24%) and *Picea* (15–25%), while *Pinus* does not exceed 30% and Poaceae values decrease to 4–6%. *Glomus*-type and minerogenic content as well as microcharcoals decrease, while carbonates show several peaks. The number of herb pollen types remains high.



**Fig. 5** Selected pollen, NPP and microcharcoal percentages of the palynological diagram Krugloe and LOI values (presented as accumulative diagram)

In the LPZ-5 (30–0 cm, 200 years BP-present), percentages of arboreal pollen (AP) decline to 60%. Poaceae (13%), Cerealia-type (3%) and *Secale* (14%) strongly increase. *Artemisia* and *Matricaria*-type increase and a variety of herbs increase with *Plantago major-media*, *Cirsium*, *Centaurea cyanus*. Coprophilous fungal spores, *Glomus*-type and minerogenic content in the sediment increase.

## Discussion

### Vegetation history of Spasskaya Gora

Pollen record from Lake Krugloe indicates forest presence at the Spasskaya Gora during the last 3500 years, indicated by 59–93% arboreal pollen (AP). Although the most herbaceous plants have low pollen productivity and dispersal capability, NAP values in recent surface samples from forests vary between 11 and 35% and meadows between 40 and 77% in Spasskaya Gora (Shumilovskikh et al. 2020b), indicating high load of herbs pollen in modern open forests. In comparison, the pollen record Chernaya from a peat bog Paltinskoe located in a hemiboreal forest around 100 km NW of Spasskaya Gora shows that NAP values vary between 1 and 27% during the late Holocene (Shumilovskikh et al. 2020a). Pollen records from the East European forest -steppe (Shumilovskikh et al. 2018; Feurdean et al. 2021) show variation of AP values between 10 and 75% since the Middle Holocene, indicating that Spasskaya Gora was covered by forests rather than typical forest-steppe. Heterogenous local topography and presence of dry soil conditions due to underlying gypsum at Spasskaya Gora might have led to a formation of herb-rich deciduous forests on upland areas, suggested by presence of Greyzemic Phaeozems. Petrophytic steppe vegetation might have existed on steep slopes where rendzina is developed.

Between 3500 and 2800 years BP, pollen spectra indicate the presence of forests with pine, birch, spruce, fir and elm. High values of *Ulmus* and *Picea* are remarkable. *Ulmus* is known to produce low amounts of pollen with moderately good dispersal that rarely travel beyond 30 km (Bradshaw and Webb 1985; Broström et al. 2008), while Abraham et al. (2014) report high pollen productivity estimates (PPE) for *Ulmus* in Czech Republik. Surface samples from Spasskaya Gora show 1% of *Ulmus* in moss pollen spectra collected from plots lacking elms in 100 m radius and <1% in 1 km radius (Shumilovskikh et al. 2020b). Today, the shore of Lake Krugloe is overgrown by *Ulmus laevis* stands, which, however, results in just ~5% of *Ulmus* pollen on the top core sample. High values up to 26% very likely indicate forests with a high proportion of elm growing in the vicinity of the lake. It is also possible that the uplands supported forests dominated by elm. The grey-luvic phaeozems in the upland areas are usually formed by deciduous forests with a herb-rich layer (Shoba 2011).

*Picea* is a moderate pollen producer with moderate pollen dispersal that is lower than that of pine (Broström et al. 2008). The top sample of the studied core has 9% spruce and 2% fir, reflecting the low proportions of these taxa in Spasskaya Gora. This is in accordance with the surface sample studies with rare presence of *Abies* and *Picea* pollen varying between 1 and 6% in the plots without fir and spruce in 100 m radius and just few trees in one km radius (Shumilovskikh et al. 2020b). *Picea* reaching 30% and *Abies* with 4% between 3500 and 2800 years BP strongly suggest the presence of hemiboreal forests in the vicinity of the lake to much larger extent than today.

High Poaceae values together with *Senecio*-type, *Cirsium*, *Sanguisorba officinalis* and *Phyteuma*-type indicate the presence of meadows or steppe meadows. High microcharcoal percentages are related to an increased fire activity, while few types of coprophilous fungi suggest presence of herbivores. *Glomus*-type is a spore of the mycorrhizal fungi Glomeromycota, growing on plant roots. Its increase, together with a higher proportion of minerogenic content in the sediment indicates enhanced soil erosion (Kofaczek et al. 2013; Shumilovskikh and van Geel 2020; Van Geel 1978). Taken together, these indicators strongly suggest anthropogenic activities close to the lake such as lumbering, pasture or haymaking, leading to overall openness of the study area. In contrast to our observations, the known Late Bronze Age settlements are about 30 km from the lake (Fig. 3). Most possibly further archaeological investigations will bring a discovery of new sites closer to the study site.

During the period 2800–2200 years BP, the forest recovers with an increased proportion of pine and birch and a decline in elm and spruce. Denser forests around the site are indicated by a decrease in the percentages of grasses and lower diversity of herbs. Forest growth might have reduced soil erosion. Fires reduced strongly at this time. Most possibly, the area was abandoned for about 600 years. *Ulmus* experienced a decline, possibly due to a general climate cooling in the late Holocene.

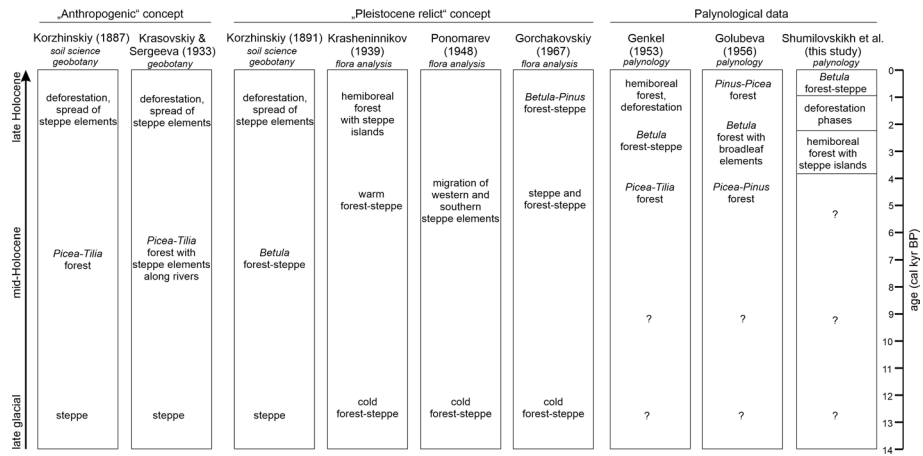
The next occupation phase started at 2200 years BP, correlating well with the spread of the Early Iron Age Glyadenovo culture in the surroundings (Fig. 3). Anthropogenic activities such as deforestation causing further decline in pine and elm, spread of meadows and pasture, increased soil erosion and enhanced fire activities are suggested from palynological data. An intensification of activities occurred between 1600 and 1000 years BP, corresponding to the establishment of Nevolino culture sites at Spasskaya Gora (Fig. 3). Although Cerealia-type includes a range of wild species producing large pollen grains (Beug 2004), values of ~1% together with increased charcoal likely indicate the presence of slash-and-burn agriculture in the vicinity of the lake. Applying low PPE of Cerealia-type estimated for forest-steppe regions (Grindean et al. 2019) results in large cropland cover by REVEALS reconstructions (Feurdean et al. 2021). In general, strong anthropogenic deforestation and transformation to cropland are known from the Central and East European forest-steppe in the Early Iron Age (Shumilovskikh et al. 2018; Feurdean et al. 2021).

The period between 1000 and 200 years BP is characterized by decreasing human impact. Forest recovery with pine, birch and spruce occurred, the landscapes were less open. This reduced the soil erosion. However, a rather high amount of charcoal, high values of Poaceae and a high number of herbaceous pollen types indicate continuing anthropogenic activities in the surroundings.

The last opening up of the landscapes occurred in the last 300 years, correlating to the Russian colonisation. This period is characterized by the strongest deforestation with a reduction in spruce, pine and birch. The spread of meadows is indicated by an increase in Poaceae and diverse herb pollen assemblages. A strong increase in Cerealia-type, *Secale* and the presence of *Centaurea cyanus* suggests large areas with arable fields with rye and other cereals at Spasskaya Gora. Historical data demonstrate that industrial development and rapid population growth led to a massive deforestation of the pre-Ural region during the eighteenth century (Yastrebov 1970; Neulybina 1970). Ancient forests were quickly disappearing especially along the rivers through intensive deforestation, frequent fires, spreading of agriculture and widespread grazing (Siuzev 1912).

To sum up, palynological data indicate that the landscapes of Spasskaya Gora were largely forested during the Late Holocene. Opening of the vegetation ~3500–2800, 2200–1000 and 200 years BP-present strongly correlates with human presence and





**Fig. 6** Overview of the concepts and palynological data to the Holocene vegetation history of the Kungur forest-steppe

anthropogenic activities such as lumbering, agriculture, grazing and haymaking. The modern *Pinus* and *Betula*-dominated forests as well as strong opening of the vegetation appear in the last 300 years and are caused by increased human activity.

### Evaluation of the concepts on the origin and development of the Kungur forest-steppe

The Tertiary as well as the Pleistocene vegetation history of the Kungur forest-steppe has so far not been palynologically studied. However, the suggested vegetation history during the Holocene can be evaluated (Fig. 6). Few existing radiocarbon-dated records from the Perm region cover the period over the last ~ 11,000 years (Elovicheva 1991; Demakov et al. 2016; Lapteva et al. 2017; Zaretskaya et al. 2020; Shumilovskikh et al. 2020a). The data suggest the presence of the open pine–birch–spruce forests during the early Holocene until ~ 8000 years BP. Most possibly, Siberian type pine–birch–spruce forest-steppe was widespread in the pre-Urals during the late glacial. The forest-steppe species might have been widespread in the region, supporting the idea of the late Pleistocene/early Holocene migration suggested by Ponomarev (1948; Fig. 6). Record from Paltinskoe peat bog (Shumilovskikh et al. 2020a) demonstrates the spread of spruce and a gradual arrival and spread of alder at ~ 7500 years BP, elm at ~ 7200 years BP, and hazel, oak and lime after ~ 6800 years BP. Broadleaved trees probably migrated from local refugia in the Urals. Finally, fir arrived from Siberia at ~ 4000 years ago. Pollen record Osintsevo located close to the Kungur forest-steppe (Fig. 1) shows dominance of pine and birch during the entire Holocene (Elovicheva 1991). In contrast to the suggested mid-Holocene migration wave (Ponomarev 1948; Fig. 6), the well-dated records from Upper (Zaretskaya et al. 2020) and Middle Kama (Shumilovskikh et al. 2020a) do not show any long-term dry phases that could cause a northward spread of the steppe vegetation. Nevertheless, both datasets reveal a maximum of broadleaved deciduous trees between 4700 and 3400 years BP in the Upper and 4000 and 2300 years BP in the Middle Kama regions, indicating rather warm climate conditions. If the migration of warm-steppe species is unlikely during the mid-Holocene,

earlier migrations of these species during the Pleistocene have to be considered. In the Kungur forest-steppe, warm-steppe species might represent relicts of long-term persisting populations similar to European steppe outposts (Kirschner et al. 2020). This issue is highly relevant for conservation purposes and should be tested by studies on macroremains, ancient DNA and population genetics.

The archive from the Lake Krugloe sheds light on the late Holocene vegetation history of the northern border of the Kungur forest-steppe. The palynological data demonstrate that during the last 3500 years, the landscapes at Spasskaya Gora were covered by hemiboreal forests with spruce, fir, pine and birch. This observation supports the ‘anthropogenic’ hypothesis, suggesting dominance of the hemiboreal forests during the Holocene (Fig. 6). However, in comparison to the typical hemiboreal forests (Shumilovskikh et al. 2020a), the forests around Lake Krugloe had either a more open or mosaic character and broad-leaved deciduous species *Ulmus*, *Tilia*, *Quercus*, *Corylus* were more abundant. Especially elm forests were widespread between 3500 and 2800 years BP. The heterogeneous relief with steep slopes allows non-woody vegetation to persist. The gypsum strata of the Kungur series of the Permian geological period causes high water permeability and therefore rather dry edaphic conditions, providing the best growing conditions for forest-steppe species (Bankovskiy 1983; Ovesnov 2009b).

The taxonomical resolution of the pollen record does not allow justification of distinctive forest-steppe species present in the past. The majority of pollen taxa indicative for the forest-steppe vegetation include entomophilous plant species with very local pollen distribution (Supplementary Table). It is reflected well by the pollen diagram from Krugloe showing mainly anemophilous taxa. From indicative forest-steppe taxa, *Adonis vernalis*, *Asparagus officinalis*-type, *Helianthemum nummularium*-type and *Sanguisorba officinalis* occur or increase during the Early Iron Age deforestation phase (Fig. 5), indicating important human role in creation of open habitats suitable for forest-steppe species. Surprisingly, the palynological record from Lake Krugloe reveals the presence of *Pulsatilla alpina*. In comparison to *Pulsatilla patens* and *P. flavescens*, which have pollen morphologically belonging to *Ranunculus acris*-type, *P. alpina* produces characteristic pericolpate microechinate pollen grains (Beug 2004). According to Baladehi et al. (2013), several other species of *Anemone* and *Pulsatilla* produce similar pollen types: *A. coronaria*, *A. biflora*, *A. tschernjaewii* and *P. albana*. Pollen of *P. alpina* is documented by the Krugloe record at approximately 1500 years ago, suggesting the presence of further pollen-producing species of *Anemone* or *Pulsatilla*, which is not present at Spasskaya Gora today.

High values of *Ulmus* are most possibly a local phenomenon of the Spasskaya Gora. Peat pollen records near the village of Kriukovy (Genkel 1957) and near Kishert (Golubeva 1956) show high values of *Tilia* and both *Ulmus* and *Tilia*, respectively. Originally, these records were correlated to the Blytt–Sernander classification and suggested to cover the entire Holocene. However, almost all records show continuous presence of *Abies*, which migrated to the Middle Kama region from Siberia between 4000 and 5000 years ago (Shumilovskikh et al. 2020a; Monika Schmidt unpubl.). Therefore, we assume that the age of these peats should not be much older than 5000 years BP. In this case, spread of *Betula* forests suggested by Genkel (1957) and Golubeva (1956) could correspond to the Early Iron Age anthropogenic activities and have secondary character (Fig. 6).

The palynological data of Lake Krugloe provides a very important message with respect to the formation of the modern forest-steppe landscapes. Distinctive vegetation opening phases and spread of forest-steppe elements correlate with more frequent fires, higher erosion and grazing (Fig. 5). Taken together, they indicate increased human activities in the past that are also confirmed by archaeological data. This speaks in favour of the

“anthropogenic” hypothesis, suggesting the establishment of secondary birch forests and spread of forest-steppe species in the deforested open landscapes. A reduction in human impact led to forest recovery. Finally, pollen data clearly show that the modern forest-steppe-like vegetation with birch and pine forest patches developed over the last 300 years and should be defined as human-made.

## Implementation for nature conservation

Today, a network of protected areas on the territory of the Kungur forest-steppe includes 33 defined areas with a total area of 25.8 thousand hectares, which covers ~3.8% of the area. However, only 20 areas with a total of 300–400 ha include steppe or forest-steppe ecosystems. In most cases, areas of steppe or forest-steppe communities are quite small, < 20 ha. Sannikov et al. (2014a, b) consider the current level of steppe ecosystem conservation to be insufficient. According to the Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets (Strategic Plan 2011), at least 17% of terrestrial ecosystems must be covered by a network of protected areas by 2020. According with EU Biodiversity Strategy (2030) at least 30% of the land should be protected by 2030. In 2018–2019, the proportion of protected areas in the world was 14.9% (UNEP-WCMC, IUCN and NGS 2018). In the Russian Federation it was 14.6% (Gosudarstvennyi doklad 2019) and only 10.7% in the Perm region. Within the Perm region, the protected areas are distributed unequally and just 3.8% of the total protected area is located in the Kungur forest-steppe (Buzmakov 2020). According to the plan, new protected areas in the Kungur forest-steppe have to cover over 1000 ha of well-preserved steppe communities (Buzmakov et al. 2011; Sannikov and Buzmakov 2015; Sannikov 2019).

In accordance with the guiding principle for preservation of biological and landscape diversity in Russia (Ob okhrane 2002, 2009), two forms of protection are implemented in the Kungur forest-steppe. The main form is a creation of protected areas for places with high nature conservation significance. Here, special rules for management of natural resources are implemented, strictly prohibiting ploughing, mining, campfires, construction activity but allowing ecological tourism and education, and reconstruction of existing buildings. The second form is a conservation of habitats of rare and endangered species. According to current legislation (Ob utverzhdenii 2009), human activities with a negative impact on these species are excluded. The identification and monitoring of the state of the habitats of these rare species is ensured by annual surveys to update the Red lists of Perm Region and Russia. A further potential step is the conservation of valuable soils. In the Kungur forest-steppe, such rare soils are grey and dark-grey soils (Greyzemic Phaeozems) (Eremchenko et al. 2010, 2015). The approval of the Red List of soils of the Perm Region and declaration of protection for valuable soils is planned for the near future.

The numerous studies at Spasskaya Gora and Podkamennaya Gora demonstrated that these areas represent one of the most important clusters for the preservation of the Kungur forest-steppe (Belkovskaya 1983; Gorchakovskiy 1967; Kerzhentsev and Anikina 1960; Korzhinskiy 1887, 1891; Ponomarev 1948; Shilova 1983). As a result, the natural monuments “Spasskaya gora” and “Podkamennaya gora” were declared in 1965 and 1981, respectively, and both areas were merged to one protected area “Spasskaya i Podkamennaya gory” in 2008 (Sannikov et al. 2017; Stenno 2006).

The danger of excessive human activities for steppe communities at Spasskaya Gora was documented by botanical surveys in 1976–1977 and 1980–1990 (Stenno 2006).

These studies recognized factors causing the degradation of steppe ecosystems, such as ploughing of virgin steppe areas, unauthorized road building, overgrazing, campfires, and gathering of medicinal plants. A special danger is the process of synanthropization of the meadow and meadow-steppe phytocenoses. A strong need for the protection of the forest-steppe plant associations led to a total prohibition of pasturing in some protected areas of the Kungur forest-steppe at the end of 1990s (Stenno 2006). However, this led to a degradation of steppe communities through the suppression of typical steppe species by mesophyte meadow species and trees. Further active management strategies have not yet been implemented.

The results of our palaeoecological investigations from Lake Krugloe strongly suggest that the absence of human activities leads to a rapid spread of forests and a reduction of open vegetation. And vice versa, moderate human impact in the past in the form of deforestation, fires, grazing or haymaking played an important role for maintaining the open vegetation of Spasskaya Gora, providing new habitats for the spread of steppe species. Based on these data, we conclude that the prohibition of any anthropogenic activities in the protected landscape will lead to loss of diversity of steppe assemblages in mid-term. Modern (Abdullin and Shikhov 2019; Shalaumova et al. 2010; Shikhov et al. 2020) and future (Feng et al. 2019) increases in precipitation in the Urals make the problem of steppe protection more difficult to solve. We emphasize that conservation of high plant diversity has to include disturbance factors in the form of selective lumbering, prescribed fires, moderate grazing or traditional mowing management. They will contribute to a mosaic-like landscape and generate open habitats for a diversity of light-loving steppe plants. For example, Erdős et al. (2018b) emphasize the importance of the preservation of habitat heterogeneity provided by a mosaic structure of grasslands and forests for the preservation of high diversity of forest-steppe vegetation. Furthermore, organic accumulation in soil typical for herbaceous phytocenoses increases the amount of humus, mineral forms of nitrogen, humidity, and acidity as well as reducing carbonates. In such conditions, steppe species are less competitive and can be replaced by meadow and forest species. Therefore, disturbances in form of mowing, grazing and prescribed fires lead to the removal of dead plant material, supporting steppe vegetation.

These disturbances have their pros and cons. Mowing is a purely anthropogenic process and should be implemented carefully. Heavily mechanized haymaking in early summer can lead to the disappearance of plant species that produce their fruits and seeds in late summer. However, traditional haymaking in late summer or early autumn is an established method for conservation of steppe ecosystems (Filatova 2016). Although haymaking or moderate grazing contributes to increase and sustain plant diversity in xerophytic steppe (Mirkin and Naumova 2014), it is not always sufficient to preserve steppe associations in mesophytic steppe. For example, studies in the Central Chernozem Natural Reserve demonstrate that mowing of areas over 100 years does not protect steppe species from replacement by meadow species, which is explained by establishment of more humid conditions during the last 50–60 years (Bobrovskaya et al. 2014, 2018).

Moderate grazing contributes to an increase in plant diversity by suppressing dominant species (Filatova 2016; Mirkin and Naumova 2014). Musina (2003) emphasizes that horses are the best means of sustainable management for xerophyte associations in Bashkortostan, cattle are less favourable, and sheep pasturing leads to the strongest degradation. Brandmayr et al. (2002) consider cattle grazing and burning as the most effective rejuvenation methods for *Stipa austroitalica*. However, overgrazing can easily lead to degradation of plant communities by decreasing plant diversity, vegetation cover, height of herbs and

grasses and by causing the spread of weeds and intensifying soil erosion (Mirkin and Naumova 2014; Morozova 1985).

The positive influence of fires on animals, plants and soil fertility has been shown by multiple studies of grassland ecosystems (e.g. Basov and Zakharova 2002; Beal-Neves et al. 2020; Smelianskiy 2015). Fire is successfully used in the steppe natural reserves “Galich’ya gora” (Danilov and Nedosekina 2005), “Mikhailovskaya tselina” (Tkachenko 1999; Tkachenko and Lisenko 2005) and “Askanii-Nova” (Shalyt and Kalmykova 1935). The decrease in the natural frequency of wild fires in the western USA at the end of the nineteenth century led to the overgrowth of the steppe by juniper (Miller and Rose 1999; Davies et al. 2019). However, many studies report a negative influence of wild fires on steppe biocenoses. In southern xerophytic steppe, pyrogenic damage has long-term consequences. Strong vegetation transformation has been documented at frequencies of one or more fires in 3 years and in the middle of the growing season (Smelianskiy 2015). A decrease in soil fertility and stability was observed over 2–3 years after fire in the xerophytic steppes of the southern Urals (Galaktionova and Vasilchenko 2019). In addition to overgrazing and climate change, wildfires might have caused the regional degradation of steppes in Mongolia (Liu et al. 2013).

Although the data of our study strongly suggest integrating disturbance into management strategies for the protection of the highly diverse Kungur forest-steppe, the elaboration of a specific regime in the protected landscape ‘Spasskaya and Podkamennaya Gory’ requires special studies and scientific assistance. The choice and combination of methods, as well as their timing and frequency, has to consider individual features of vegetation assemblages, their relief and forest proximity.

## Conclusions

Our revised interpretation of the history of the Kungur forest-steppe can be summarised as follows. The presence of numerous relict species and endemics indicates a long and complicated history of the flora formation during the Pleistocene. The gypsum strata of the Kungur series of the Permian geological period is highly water permeable, causing rather dry edaphic conditions and allowing the survival of steppe species within the boreal zone. Southern-facing outcrops are important habitats, possibly playing the role of ‘interglacial refugia’ for steppe elements during the Holocene and earlier interglacials. Palynological data provide strong evidence that the modern Kungur forest-steppe with a mosaic of *Betula* and *Pinus* forest patches versus meadows and steppe meadows is man-made. In the second half of the Holocene, the majority of the landscapes were covered by hemiboreal forests with a high proportion of deciduous trees, while steppe vegetation was most possibly restricted to south-facing outcrops and slopes. Human activities led to strong deforestation, giving some steppe species a chance to spread in the area and providing a typical ‘forest-steppe’ character to the vegetation.

The results of our study strongly suggest that moderate human impact in form of deforestation, fires, pasturing or mowing played an important role in maintaining the open vegetation of Spasskaya Gora. Therefore, the prohibition of any anthropogenic activities in the protected landscape will lead to loss of diversity of steppe assemblages in the mid-term. Conservation of high plant diversity requires disturbance in the form of selective lumbering, prescribed fires, moderate grazing or traditional mowing. The specific management

regime should be developed with further scientific assistance to tailor it to the vegetation in the protected area.

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**Data availability** All data will be submitted to PANGAEA after publication.

**Code availability** Not applicable.

## Declarations

**Conflict of interest** Not applicable.

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